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THE *ANOPHELES LEUCOSPHYRUS* GROUP.[1]

By Donald H. Colless, B.Sc.Agr., F.R.E.S.[2]

(*Department of Parasitology, University of Malaya.*)

Manuscript received 8th February, 1955.

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PART I. SYSTEMATICS.

1. Introduction.

In the following pages an attempt is made to systematise our knowledge of the *A. leucosphyrus* group of Anopheline mosquitoes. The first section aims at giving reasonably full descriptions of all forms[3] known to exist within the group,

[1] Publication of this paper has been greatly facilitated by generous financial assistance from the Colonial Medical Research Committee and the University of Malaya.

[2] Formerly *Entomologist, Borneo Malaria Research, Labuan, North Borneo,* where this study was commenced and much of the material collected.

[3] The neutral term "form" is used throughout for any homogeneous population where reference to a definite systematic category is not desired.

together with notes on their identification, distribution, and probable relationships, while the biology of these forms is dealt with in the second section. While most of the work is original, material has been gathered from all possible sources and the work as a whole represents an extension of that commenced by Reid (1949) in his valuable preliminary account of the group.

The *A. leucosphyrus* group is here defined as comprising all those members of the group *Neomyzomyia* which possess, in the adult stage, a conspicuous white band covering the tibio-tarsal joint of the hind leg. They form a clear-cut and homogeneous group confined to the Oriental region, showing various degrees of morphological and biological similarity but all obviously related and derived from a common ancestral stock. The term " group ", in the sense of " species-group ", appears to be the best available to describe this relationship, despite its alternative formal usage for the systematic category inferior to the sub-genus. The term " sub-group ", used by Baisas (1938), is now in general use as a definite category, *e.g.* Knight and Marks (1952) ; it could be employed here, but would necessitate defining the remaining sub-groups within the group *Neomyzomyia*, a task beyond the scope of this paper. Other terms available, such as " super species " and " complex ", imply, by modern usage, relationships rather different from that intended in this instance. The term " group " then, as used here, refers to a presumably monophyletic assembly of species and lower categories, which are limited to a definite geographic area, and which, by virtue of distinct morphological and biological similarities, are conveniently separated, as a group, from other related forms. Throughout this paper, the name *A.* " *leucosphyrus* " in quotes refers to the group as a whole, or to forms whose exact identity has not been recorded : this useful convention was introduced by Reid and Hodgkin (1950) and Reid (1953) for the *A. umbrosus* and *A. hyrcanus* groups.

It has long been known, or suspected, that *A.* " *leucosphyrus* " is a vector of malaria and the first record of natural infection appears to have been made by Bais (1920) in Sumatra. Little attention seems to have been paid to early records, but during the last 12 years investigations by Clarke and Choudhury (1941), McArthur (1947), Kuitert and Hitchcock (1948), and Macan (1948), to name only a few, have made it abundantly clear that *A.* " *leucosphyrus* " is a dangerous vector over a large part of the Oriental region—in Assam, Burma, Indo-China, Sumatra, Borneo, and Celebes. A comprehensive review of this work is given by McArthur (1951).

Together with, and subsequent to, these epidemiological studies, systematic research has been revealing an ever-increasing complexity within what was originally regarded as a single species, the *A. leucosphyrus* of Dönitz (1901). As long ago as 1903, *A. elegans* was described as a separate form, but by 1912 it had been sunk as a synonym of *leucosphyrus* and a further 37 years passed before it was finally recognised as distinct, by Reid (1949). In 1921, " var. *hackeri* " was described from Malaya by Edwards and in later years the " variety " came to be recognised as a species by some workers, *e. g.* Gater (1934). The Philippine forms were investigated by Russell and Baisas (1936), Baisas (1936*a* and 1938) and King and Baisas (1936) and three new forms were described " var. *balabacensis* ", " var. *riparis* " and *A. cristatus ;* a fourth form from Luzon was identified as the type. The latest addition to the group, *A. pujutensis*, was described from Borneo by the writer (Colless, 1948), while Reid (1949), in a preliminary revision,

produced new distribution records and evidence for the reinstatement of *elegans*, the sinking of *balabacensis* as a synonym of the type, and the recognition of the *A. hackeri* of Celebes as a distinct form; he also suggested that most of the "varieties" would be found to be good species. Finally, Bonne-Wepster and Swellengrebel (1953) have collected together much of the available information on the group.

In the light of present knowledge it appears that the group may be divided into at least 13 species, subspecies, and forms of doubtful status, and of these a number have been recognised subsequent to the epidemiological studies mentioned above. This fact has had two main consequences. Firstly, an obvious explanation is seen for the reputation of *A.* "*leucosphyrus*" as a harmless mosquito in some areas and a dangerous malaria vector in others. Secondly, it has become a matter of importance to establish the identity of the vectors and the means for their recognition. Reid (1949) examined the small amount of evidence then available and suggested that suspicion fell most heavily on the type form, under which he included "var. *balabacensis*". More recently Colless (1950) has shown that the vector in North Borneo, and probably some other areas, is this latter "variety", and Zulueta and Colless (unpubl.) have shown that the type form, *A. l. leucosphyrus*, is an important vector in Sarawak. The evidence is further examined in Part II of the present paper.

A further problem has been raised by the fact that certain forms have hitherto been inseparable in their larval stages, thereby severely limiting the usefulness of larval surveys in areas where such forms occur together. Much of the work in this paper has been aimed at discovering characters for larval identification and a measure of success has been obtained.

The intention throughout has been to adopt a system of nomenclature, and a species concept, in accordance with modern trends in systematics, as outlined by such authors as Huxley (1942) and Mayr (1942). The species is here regarded as an assembly of local populations, all actually or potentially interfertile, but, in nature, reproductively isolated from all other forms. Where two or more forms occur sympatrically, *i.e.* in close contact over the same area, without showing any loss of identity, it is assumed that no inter-breeding occurs and that the forms are therefore specifically distinct. It is, of course, sometimes impossible to apply such a yardstick for direct measurement and, in such cases, only morphological criteria can be employed. This, and general lack of information, has necessitated certain arbitrary decisions which are discussed in detail in the text.

2. Terminology and Abbreviations.

The morphological terminology used is that of Christophers (1933), but certain conventions have been adopted: (i) Roman numerals are used to designate abdominal segments and Arabic numerals for hairs; thus hair IV.13 refers to hair No. 13 on abdominal segment IV; (ii) a pair of figures separated by a colon refers to the branching of the same hair on opposite sides of the body; (iii) a pair of figures separated by a dash refers to a statistical range; (iv) such terms as "often", "occasionally", etc., are usually qualified by showing, as a fraction in brackets, the actual proportion of specimens found to possess the character in question; (v) in describing the apex of the male abdomen, the terms "ventral" and "dorsal" refer to the apparent position after rotation.

Certain measurements and ratios require explanation :

(i) Adult palps and proboscis are measured from the level of the ventral setae basally to the apices of the fourth segment and labellae respectively.

(ii) Wing length is measured from the extreme base of the costa, direct to the furthest apical point, excluding the fringe.

(iii) Larval antennae are measured from the extreme base of the shaft to the base of the dorsal sabre-piece.

(iv) The " Toothed-Margin Index " (T.M. index) of the pupal paddle is a convenient modification of the " Refractile Index " of Crawford (1938) and expresses the ratio (a/b) of two lengths, (a) from the tip of the inner basal tubercle to the base of the most distant marginal tooth, and (b) from the same point to the base of the paddle hair. (*See* fig. 6.)

(v) The anterior and posterior forked-cell petiole indices are the ratios of the length of veins 2 and 4 to veins 2.2 and 4.2 respectively ; the forked-cell index is vein 2 divided by vein 4. Veins 2 and 4 are measured from point of bifurcation to the junction of the nearest cross-vein.

Certain abbreviations have been used throughout and due apology is offered. In view of the many cumbersome terms to which frequent reference is made, it is felt that the space saved thereby justifies their use. They are as follows :—

(i) *The wing* :

PHP—prehumeral pale spot.
PSP—presector pale spot.
SP—sector pale spot.
ASP—accessory sector pale spot.
SCP—subcostal pale spot.
af.—anterior forked-cell.
HD—humeral dark spot.
PSD—presector dark spot.
MD—middle dark spot.
PAD—preapical dark spot.
AD—apical dark spot.
pf—posterior forked-cell.

(ii) *The larval head* :

ic—inner anterior clypeal hairs.
oc—outer anterior clypeal hairs.
pc—posterior clypeal hairs.

Simple statistical analyses have been made of some quantitative data, using the " t " and " χ^2 " tests. These were made in the usual manner, as outlined by such authors as Snedecor (1946) and the results are given according to standard convention. The terms " significant " and " highly significant " as used, refer to maximum probabilities of 0·05 and 0·01 respectively of the observed differences being due to chance alone.

Illustrations are all based on camera-lucida sketches of actual specimens ; slight corrections have been made of distortion due to drying, flattening, etc., in preserved specimens.

3. Systematic List of Forms Described.

The group has been divided into the 13 forms listed below but, for reasons explained in the text, five have been left for the present with vernacular names only.

A. leucosphyrus leucosphyrus Dönitz, 1901. Sumatra, Malaya, Borneo.
A. leucosphyrus balabacensis Baisas, 1936. S. Philippines to S.W. India.
A. leucosphyrus, " Luzon form ". Luzon Is.

A. leucosphyrus, " Negros form ". Negros Is.
A. leucosphyrus, " Fraser's Hill form ". Central Malaya.
A. leucosphyrus, " Kepong form ". Central Malaya.
A. riparis riparis King and Baisas, 1936. S. Philippines.
A. riparis macarthuri subsp. n. Borneo, Malaya.
A. cristatus King and Baisas, 1936. Mindanao Is.
A. pujutensis Colless, 1948. Borneo, Sumatra, Malaya.
A. elegans James, 1903. S.W. India, Ceylon.
A. hackeri Edwards, 1921. Malaya, Borneo.
A. " *leucosphyrus* ", " Celebes form ". Celebes.

4. Keys to the Species and Subspecies of the *A. leucosphyrus* Group.

In a group of such closely related forms, it is difficult to lay down definite key characters for the identification of every individual specimen. The keys following will give reasonable accuracy but may not give a 100 per cent. separation within certain groups; the larval key, in particular, will inevitably give a small percentage of misidentifications when applied to single specimens. The terms " usually " and " nearly always ", as used, reflect the fact that differences are frequency statistical rather than absolute and that a degree of overlap is to be expected. Nevertheless, in difficult cases, reference to the fuller descriptions will usually produce an accurate identification. No keys are given for males or pupae since these would be of doubtful accuracy and are, in any case, rarely required in practise.

Females.

1 Proboscis distinctly longer than the fore femur (ratio 1·16–1·40) and usually much longer than the palps; a narrow ring of pale scales sometimes present at the apex, proximal to the labella 2
Proboscis uniformly dark, approximately equal to, or shorter than the fore femur (ratio 0·85–1·15), and, at most, only slightly longer than the palps 5
2 Presector dark spot on vein 1 with one or more pale interruptions *" Celebes form "*
Presector dark spot on vein 1 without pale interruptions 3
3 Palps with very narrow pale bands, apical segment merely tipped with white . . . . . **hackeri**
Palps with broader pale bands, that at apex about as broad as preapical dark band 4
4 Middle and preapical dark spots of vein 1 each with only one pale interruption; hind tarsal segment IV with a prominent basal pale band. (W. India and Ceylon) . . . . . **elegans**
Middle and/or preapical dark spots of vein 1 with more than one pale interruption; basal pale band of hind tarsal segment IV very small or absent . . . . . **pujutensis**
5 Presector dark spot of vein 1 with one or more pale interruptions on at least one wing 6
Presector dark spot of vein 1 without pale interruptions 8
6 Presector dark spot on vein 1 extending basally well into the level of the humeral dark spot of the costa, or into the humeral pale spot level; hind tarsal segment IV with no basal pale band or a very small one 7

Presector dark spot on vein 1 extending basally no further than the level of the centre of the humeral dark spot of the costa, usually no further than the level of the presector pale spot; hind tarsal segment IV almost always with a prominent basal pale band (may be missing in Malayan specimens) . . . . . **leucosphyrus balabacensis** "*Negros*," "*Fraser's Hill*" and "*Kepong*" *forms.*

7 Tarsal banding reduced, bands on fore tarsi incomplete beneath, not completely encircling segments; costa without an accessory sector pale spot. (Luzon Is.) . . . . . "*Luzon form*"

Tarsal banding normal; costa frequently with an accessory sector pale spot. (Borneo, Malaya and Sumatra) . **leucosphyrus leucosphyrus**

8 Costa without a prehumeral pale spot, proboscis rather short, proboscis/fore femur ratio less than 0·90. (Mindanao Is.) . . . **cristatus**

Costa nearly always with a prehumeral pale spot; proboscis longer, proboscis/fore femur ratio greater than 0·90 9

9 Costa and vein 1 usually with a prominent accessory sector pale spot, that on vein 1 frequently continuous with the presector pale spot or separated by a very small dark spot; apical pale band of palp usually distinctly narrower than the preapical dark band; propleural hairs single. (S. Philippines) . . . . . **riparis riparis**

Accessory sector pale spot usually absent from the costa, variable on vein 1 but often separated from the presector pale spot by a dark spot of about its own length; apical pale and preapical dark bands of the palp of about the same length; propleural hairs frequently double on at least one side. (Borneo and Malaya) . **riparis macarthuri**

4th Instar Larvae.

The larvae show no definite group characters, but in all forms prothoracic hair 1 rises from a prominent, chitinised basal tubercle. The larvae of *A. watsoni*, *A. stookesi* and *A. saungi*, which also show this character, are included in the key below, while those of *A. elegans* and the "Celebes form" are still unknown. It should be noted that many characters used in the key can be clearly seen only in larval pelts, or cleared specimens.

1 Abdominal palmate hair on segment II fully developed with clearly differentiated filaments 2

Abdominal palmate hair on segment II not fully developed, with, at most, lanceolate leaflets 5

2 Posterior clypeal hairs with four or more conspicuous branches . . 3

Posterior clypeal hairs simple or with two or three branches distally . 4

3 Posterior clypeal hairs with numerous branches concentrated towards base; prothoracic hair 13 rising from beneath a chitinous plaque **stookesi**

Posterior clypeal hairs with fewer branches, rising along the shaft; prothoracic hair 13 not so . . . . . **cristatus**

4 Posterior clypeal hairs placed close to anterior clypeals, their bases forming an approximately equilateral triangle . . . . . **watsoni**

Posterior clypeal hairs placed further back from anterior clypeals, their bases forming a scalene or isosceles triangle . . . . . **hackeri**

5 Posterior clypeal hairs very long, reaching well past the anterior margin of the head; lateral hairs of abdominal segs. IV–VI 3-branched. (Borneo, above 4000 feet) . . . . . **saungi**

Posterior clypeal hairs shorter, rarely reaching anterior margin of the head; lateral hairs rarely 3-branched when posterior clypeal hairs are long 6

6 Basal tubercle of prothoracic hair 1 with a prominent apical tooth or spine 7

Basal tubercle of prothoracic hair 1 with a weak and inconspicuous tooth or none 13

7 Metathoracic palmate hair not developed as such, hair-like . "*Negros form*"

Metathoracic palmate hair partially developed, with long attenuated lanceolate leaflets 8

8 Abdominal hair I.9 with not more than four branches on either side; prothoracic hair 13 with seven branches or less 9

Abdominal hair I.9 with five or more branches on at least one side; or if 4-branched, prothoracic hair 13 with eight or more branches on at least one side 10

9 Abdominal palmate hair on seg. II very weakly developed, its branches hair-like or slightly flattened; pecten with teeth clearly separable into long and short types . . . . . "*Luzon form*"

Abdominal palmate hair on seg. II fairly well developed, usually with lanceolate leaflets; pecten teeth of various graduated lengths **leucosphyrus balabacensis**

10 Prothoracic hair 13 with seven or more branches on at least one side . 11

Prothoracic hair 13 with no more than six branches 12

11 Abdominal hair I.3 with three or more apical branches on at least one side . . . . . "*Kepong form*"

Abdominal hair I.3 simple or bifid . . . . . "*Fraser's Hill form*"

12 Abdominal hair IV.13 with three branches or less, rarely four on one side only. (S. Philippines) . . . . . **riparis riparis**

Abdominal hair IV.13 usually with four or more branches on at least one side. (Borneo, Malaya) . . . . . **riparis macarthuri**

13 Hair I.9 with four branches or less . . . . . **pujutensis**

Hair I.9 with five or more branches on at least one side 14

14 Basal tubercles of prothoracic hairs 1 and 2 fused; prothoracic hair 13 with six or less branches 12

Basal tubercles of prothoracic hairs 1 and 2 separate; prothoracic hair 13 with six or more branches . . . . . **leucosphyrus leucosphyrus**

5. Descriptions.

Since *A. l. balabacensis* is the commonest member of the group and formed the largest proportion of material available for examination, it has been described in some detail—in other forms only the more important features are mentioned. Further details, of chaetotaxy, etc., are given in Tables I and VIII–XIV.

A. leucosphyrus balabacensis Baisas, 1936.

Baisas, F. E., 1936, *Philipp. J. Sci.* **59** : 65 (*A. leucosphyrus* var. *balabacensis*).

Type locality : Philippines : Balabac, Balabac Is.

Types : Male and female in Bureau of Health, Manila.

Synonyms : "Balabac species or variety", Russell and Baisas, 1936. *A. leucosphyrus*, in part or whole, Christophers (1933), King and Baisas (1936) and others.

TABLE I.—*Larval Chaetotaxy of* A. l. balabacensis.

(Counts are taken from 10 specimens, unless otherwise indicated; means are *in italics*.)

Head.	
Hair.	Number.
Sut. . .	1–2, *1·2*
Tr. sut. .	1–3, *2·2*
13	4–7, *5·2*
14	1–2, *1·5*
15	1–3, *2·0*
Term. ant.	2–3, *2·5*

Thorax.			
Hair.	Prothorax.	Mesothorax.	Metathorax.
1	10–24,[6] *15·4*	19–34,[3] *27·0*	2–7, *4·5*
2	8–16,[2] *11·0*	1–5,[5] *3·1*	3–4, *3·3*
3	1–1, *1·0*	1–1, *1·0*	1–3, *1·8*
4	12–18, *14·3*	1–1, *1·0*	1–1, *1·0*
5	Numerous	2–3, *2·2*	23–40,[5] *32·4*
6	1–1, *1·0*	3–5, *3·6*	1–3, *2·4*
7	16–27, *20·7*	2–4, *3·0*	21–32, *28·0*
8	20–32, *26·6*	17–31,[1] *23·0*	22–38, *29·0*
13	3–10,[4] *6·0*	3–9,[3] *5·5*	2–3, *2·9*
14	4–6, *4·8*	2–6,[3] *3·7*	.

[1] From 20 specimens.
[2] ,, 30 ,,
[3] ,, 40 ,,
[4] ,, 50 ,,
[5] ,, 60 ,,
[6] ,, 70 ,,

Abdomen.								
	Segments.							
Hair.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
1	5–12,[3] *7·8*	10–22,[3] *15·8*	16–22, *19·2*	16–21, *18·7*	16–23, *18·8*	15–21, *17·8*	9–15, *11·8*	.	.
2	1–2, *1·4*	4–8, *5·9*	3–8, *5·3*	2–4, *3·0*	2–4, *3·0*	1–2, *1·1*	4–6, *5·5*	.	Post-spiracular 3–6, *4·6*

	Abdomen.								
	Segments.								
Hair.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
3	1–3,[6] *1·5*	3–6, *4·4*	3–3, *3·0*	2–3, *2·9*	2–3, *2·7*	3–5, *3·6*	2–4, *2·9*	.	.
4	5–7, *5·3*	1–1, *1·0*	1–1, *1·0*	2–4, *2·4*	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	.	.
5	2–4, *3·1*	3–6, *4·9*	3–5, *3·6*	2–4, *3·0*	2–5, *3·1*	3–6, *4·0*	3–6,[3] *4·0*	2–3, *2·1*	.
6	13–23, *17·4*	20–27, *22·5*	10–19, *13·6*	1–3, *2·0*	2–3, *2·2*	2–4, *3·0*	3–5, *3·9*	3–6, *4·8*	2–6,[4] *2·9*
7	12–19, *15·5*	13–24, *19·6*	2–5,[3] *3·9*	2–5,[3] *3·9*	3–5, *3·6*	2–3, *2·3*	2–5, *3·6*	1–1, *1·0*	.
8	.	1–3, *1·7*	1–3, *1·7*	1–4, *2·2*	2–3, *2·4*	2–3, *2·2*	2–5, *4·2*	4–8, *6·2*	2–4, *2·7*
9	3–5,[6] *3·6*	5–10, *7·0*	4–10,[5] *6·6*	5–10,[3] *6·6*	4–8,[3] *5·7*	5–8, *6·1*	2–4, *3·1*	4–9,[3] *6·0*	.
10	2–4, *2·2*	2–3, *2·3*	2–3, *2·3*	1–3, *2·2*	1–3, *2·2*	3–4, *3·4*	4–7, *5·1*	1–1, *1·0*	.
11	3–4, *3·1*	1–1, *1·0*	2–3, *2·1*	2–3, *2·1*	2–3, *2·1*	2–3, *2·2*	1–3, *2·0*	.	.
12	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	1–1, *1·0*	.	.
13	2–7, *3·9*	2–6,[3] *3·6*	3–6, *3·9*	1–4,[6] *2·9*	3–3, *3·0*	4–8, *6·1*	2–3, *2·5*	3–5, *3·4*	.

[1] From 20 specimens.
[2] ,, 30 ,,
[3] ,, 40 ,,
[4] ,, 50 ,,
[5] ,, 60 ,,
[6] ,, 70 ,,

Adult female.

Head: Labium uniformly dark, rather shaggy ventrally towards the base; length 1·5–2·4 mm., av. 1·9 mm. (63 specimens). Palps (fig. 2) with narrow apical pale bands on segs. 2 to 4 and a broader apical band on seg. 5, the latter varying from about the same width as, to almost twice the width of, the preapical dark band; palp length 1·4–2·4 mm., av. 1·8 mm. (63 specimens); ratios of lengths of segments: *3/5*, 2·2–3·3, *3/4*, 1·5–1·9 (23 specimens) (*see* Geographic Variation). Clypeus dark brown, tori light brown, both devoid of scales. Antennae with a patch of pale and dark scales internally on seg. 3. Vertex narrow with chaetae usually arranged in two rather irregular rows; erect scales of occiput white on about the anterior half, otherwise dark. Ratios (Table IX): palp/proboscis, 0·83–1·00; proboscis/fore femur, 0·99–1·14 (62 specimens). Maxillary teeth 13–16

in number, usually 13 or 14, av. 13·8 (23 specimens). Pharyngeal teeth 12–15 in number, length 0·03–0·06, av. 0·042 mm. (13 specimens).

Thorax : Integument mainly dark in fresh specimens. Mesonotum with characteristic *Neomyzomyia* pattern of paired dark spots—one in posterior angle of fossa, one behind and slightly lateral to this, and one above the wing root. In undamaged specimens, an additional pattern is formed by the greyish " bloom " covering most of the mesonotum—in certain areas this appears to be thin, or absent, producing a variable pattern which changes with the conditions of lighting. A typical dorsal view shows a central dark line and two distinct lateral lines, between the fossae ; also paired dark spots, anteriorly and posteriorly above the wing roots, and a central dark area in front of the scutellum ; the latter is dark on the central third. Pronotal lobes with a dorsal tuft of dark scales. Anterior promontory with a central tuft of narrow pale scales which extend back a short distance on the mesonotum ; also lateral tufts of broader scales, pale above and dark below. A few pale scales often present in the fossae ; also a patch of erect pale scales laterally in front of the wing roots. Halteres conspicuously white above, dark below. Setae : propleural 1 : 1 to 3 : 4, usually 2 : 2 ; spiracular usually about 2 ; lower sternopleural 1–4, usually 2 or 3 ; upper sternopleural 2–6, usually 3 or 4 ; prealar 3–6, usually 4 or 5 ; subalar 3–6, usually 3 or 4 ; with the exception of the propleurals, most of these setae are rather weak and fine, and difficult to count in pinned specimens.

Wing (fig. 1) *:* Length 3·08–4·00, av. 3·44 mm. (40 specimens). Costa with PHP on at least one wing, usually both ; an ASP may be present also (*see* Geographic Variation) ; MD a little longer than PAD, AD much shorter than either. Subcosta often with ASP. Vein 1 with PSD on at least one wing divided by 1–4 pale interruptions (usually 1 or 2), the spot about equal in length to the corresponding costal spot or extending basally into the PSP area, sometimes into the apical half of the HD area (*see* Geographic Variation) ; very rarely, less than 0·5 per cent., PSD undivided on both wings. MD of vein 1 with 1–5 pale interruptions, usually 2 or 3 ; PAD with 1–4, usually 2 or 3. In most specimens, cross vein 1–2 not apparent, vein 2 appearing to fork directly from vein 1. Apex of wing pale from AD to apex of vein 2.1, usually followed by a dark spot between veins 2.1 and 2.2, and a large pale area extending to a little past vein 3, but this area variable over part of the range (*see* Geographic Variation). Remainder of fringe dark, except for fringe spots at apices of veins 4, 5.1, usually at 5.2, and sometimes between 5.2 and 6. *af.*-petiole index 0·45–0·69, av. 0·56 ; *pf.*-petiole index 0·85–1·27, av. 1·04 ; forked cell index 1·53–2·06, av. 1·72 (37 specimens). Fork of vein 4 almost invariably a little distal to fork of vein 2.

Legs : Coxae without scales ; fore trochanters with a patch of pale and dark scales ; mid and hind trochanters apparently unscaled in pinned specimens (mounting in balsam may reveal sparse scaling). Femora and tibiae with conspicuous white speckling ; on the under surfaces, and particularly towards the bases of the tibiae, the spots tend to coalesce in large pale " splashes " ; hind femur minutely pale at apex. Tibiae with very narrow pale basal bands ; fore tibia with a pale patch externally at apex ; hind tibia with a broad apical pale band, one-fifth to one-sixth length of the tibia, which, together with the broad basal band of tarsal segment 1, forms the pale " knee spot " characteristic of the group. On its internal surface the pale apical band occasionally has a few dark scales towards the apex, but these usually appear to be loose, as though brushed from the wing or legs. Occasional specimens show a short linear extension of dark scaling into the base of the pale band on its ventral surface, but this is nowhere near so marked as in, for instance, *A. riparis* (see fig. 9). Tarsal segments : seg. 1 of all legs usually with pale speckling, sometimes a few spots on seg. 2. Fore tarsi with apical pale bands on all segments ; segs. 2 to 4 with similar basal bands ; pale bands completely encircling segments, but less well-defined on under surface. Mid-tarsi with narrow, ill-defined, apical pale bands on all segments, sometimes similar basal bands on segs. 2–4. Hind tarsi with a broad basal pale band on seg. 1, about half as long as the adjacent tibial band ; segs. 2 to 5 with distinct apical pale bands ; seg. 4 with a distinct basal pale band on at least one leg, almost always on both ; seg. 5 sometimes pale at base. Length of fore-femur 1·5–2·1, av. 1·8 mm.

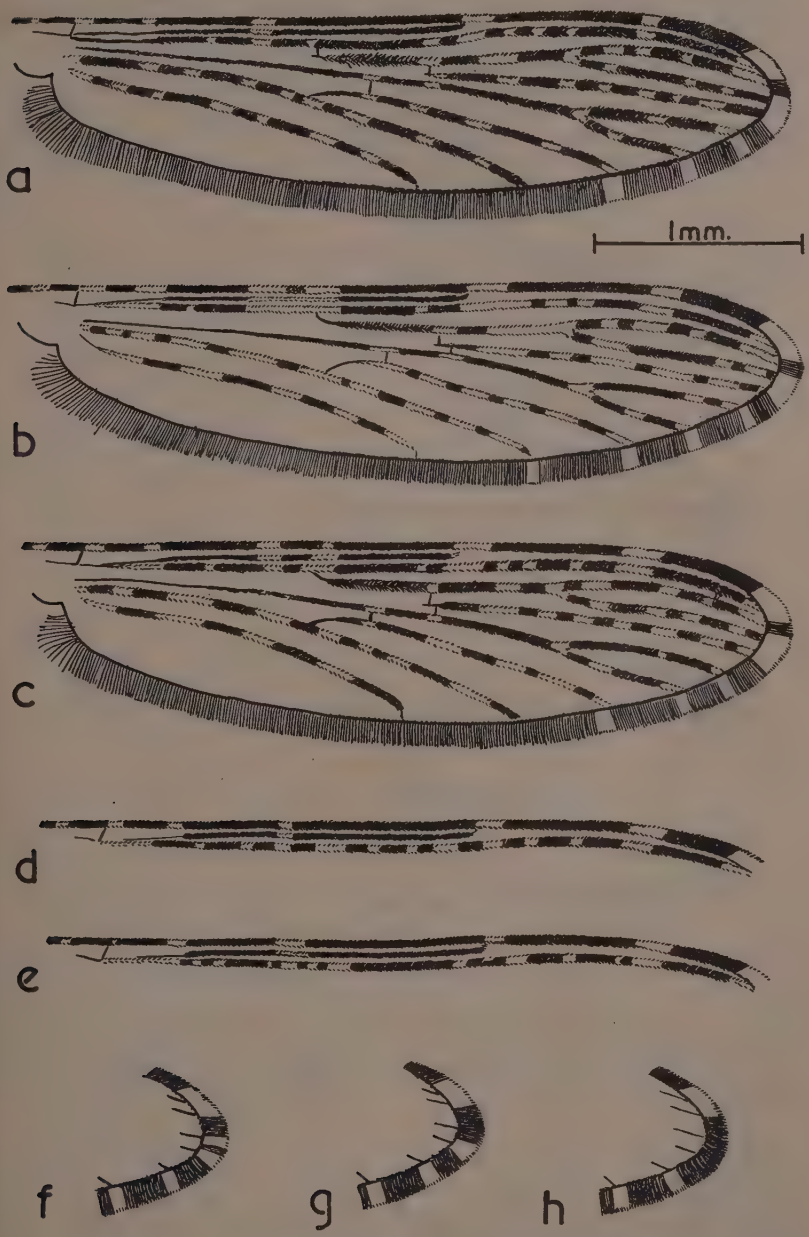

Fig. 1.—*Wings:* (*a*) "Fraser's Hill form"; (*b*) to (*h*) *A. l. balabacensis:* (*b*) Borneo, pale variant; (*c*) Borneo, normal; (*d*) N. Malaya, costa and vein 1; (*e*) Assam, costa and vein 1; (*f*) to (*h*) wing apex variation, stages 1–3 respectively.

Abdomen : Integument mainly dark but sternites with paired pale areas towards the anterior margins of segs. 3 to 7, and a central pale area anteriorly on seg. 2. Scaling reduced and rather variable : dorsally, seg. VIII with numerous golden scales, most profuse apically ; seg. VII usually, and seg. VI sometimes, with a few pale scales along apical border and several dark scales laterally ; ventrally, seg. VIII with lateral patches of sparse golden scaling ; seg. VII with a tuft of erect dark scales on apical margin ; a few dark scales sometimes present in a similar position on seg. VI, and rarely, on seg. V also.

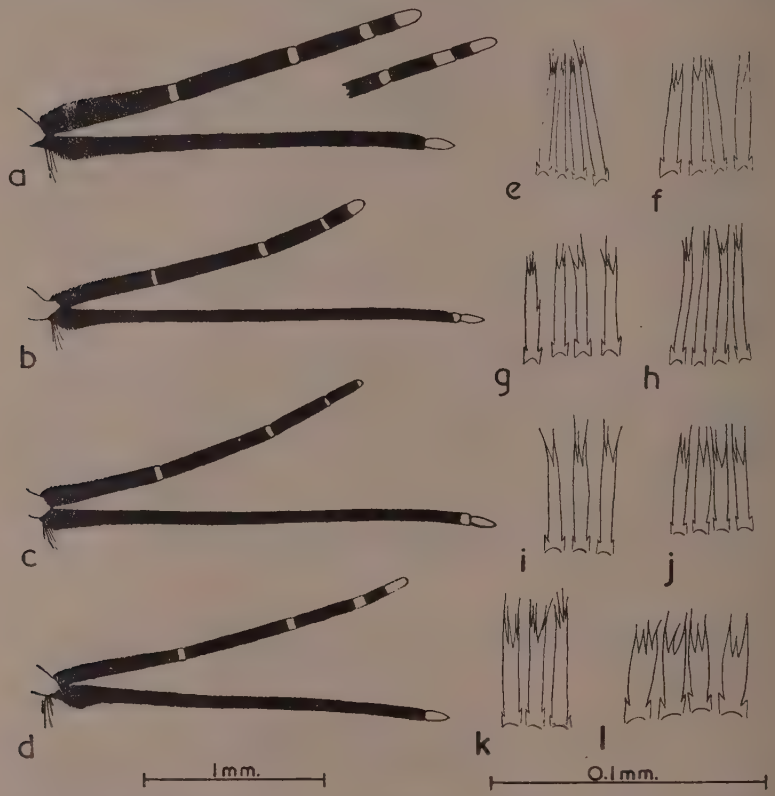

FIG. 2.—*Palps and proboscis :* (*a*) *A. l. balabacensis*, Borneo and (apex only) N. Malaya; (*b*) *A. pujutensis*, Borneo ; (*c*) *A. hackeri*, Borneo ; (*d*) *A. elegans*, Ceylon.
Central phayrngeal teeth : (*e*) " Fraser's Hill form " ; (*f*) *A. l. balabacensis*, Assam ; (*g*) *A. l. balabacensis*, Borneo ; (*h*) *A. l. leucosphyrus*, Malaya ; (*i*) and (*k*) *A. pujutensis*, paratypes ; (*j*) *A. hackeri*, Borneo ; (*l*) *A. riparis macarthuri*, Malaya.

Adult male.

In general, similar to the female.

Head : Proboscis rather long, 2·1–2·5, av. 2·3 mm. (9 specimens). Ratio proboscis/fore femur 1·34–1·57, av. 1·46 (15 specimens).

Thorax : Propleural setae 1 : 1 to 2 : 3, usually 2 : 2 (24/31).

Wing : Length 2·9–3·7, av. 3·3 mm. (15 specimens) ; generally paler than in the female

with reduced scaling. PSD of vein 1 more often complete, without pale interruptions on either wing (3/25).

Legs : Tarsal banding rather reduced ; segments of fore tarsi rarely (2/20) with basal bands. Length of fore femur 1·5–1·7, av. 1·5 mm. (9 specimens).

Abdomen : Resembles female, but seg. VIII with more profuse golden scaling on the dorsal surface, and numerous dark scales ventrally.

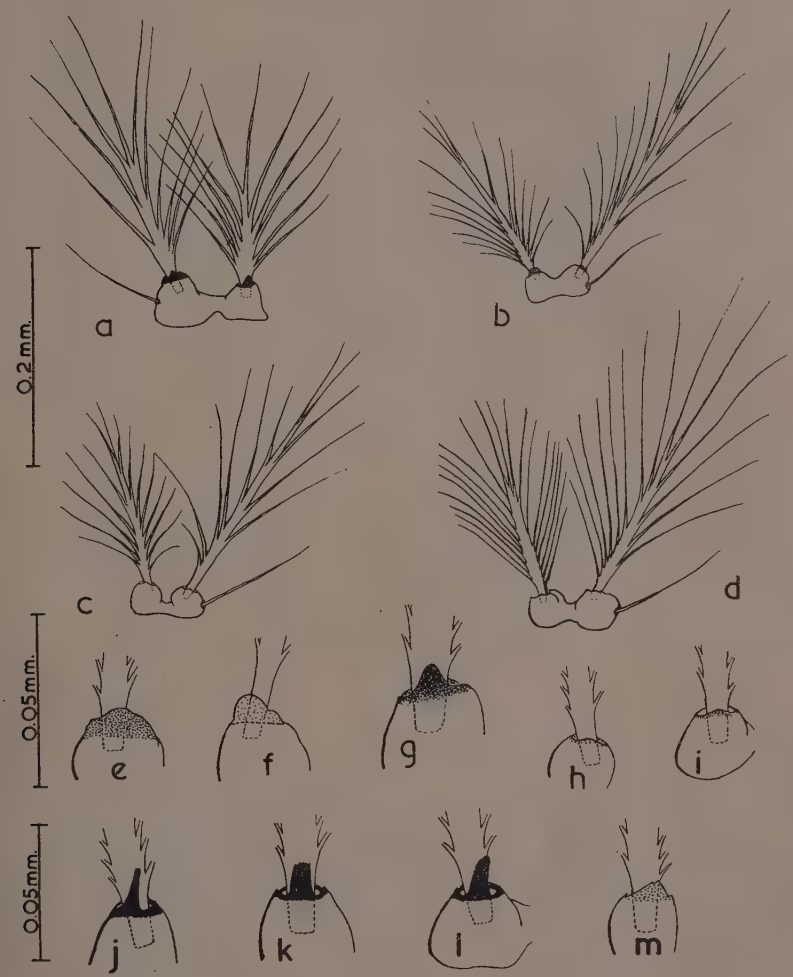

Fig. 3.—*Shoulder hairs :* (*a*) *A. l. balabacensis*, Borneo ; (*b*) *A. riparis macarthuri*, Malaya ; (*c*) *A. pujutensis*, Borneo ; (*d*) *A. hackeri*, Borneo.

Basal bosses, inner shoulder hairs : (*e*) *A. riparis riparis*, Mindanao ; (*f*) *A. r. macarthuri*, Malaya ; (*g*) "Luzon form" ; (*h*) *A. pujutensis*, Borneo ; (*i*) *A. l. leucosphyrus*, Malaya ; (*j*), (*k*), (*l*) *A. l. balabacensis*, Borneo ; (*m*) *A. hackeri*, Borneo,

Terminalia: Coxites with profuse scaling. Phallosome with 13–19 blade-like leaflets, usually about 8 on either side; some leaflets with a variable degree of serration on one, rarely both, edges; length of leaflets 0·04–0·06, av. 0·049 mm. (8 specimens). Harpago with the apical seta slightly shorter than the club, and usually one, sometimes 2, shorter internal setae; club occasionally double (1/8).

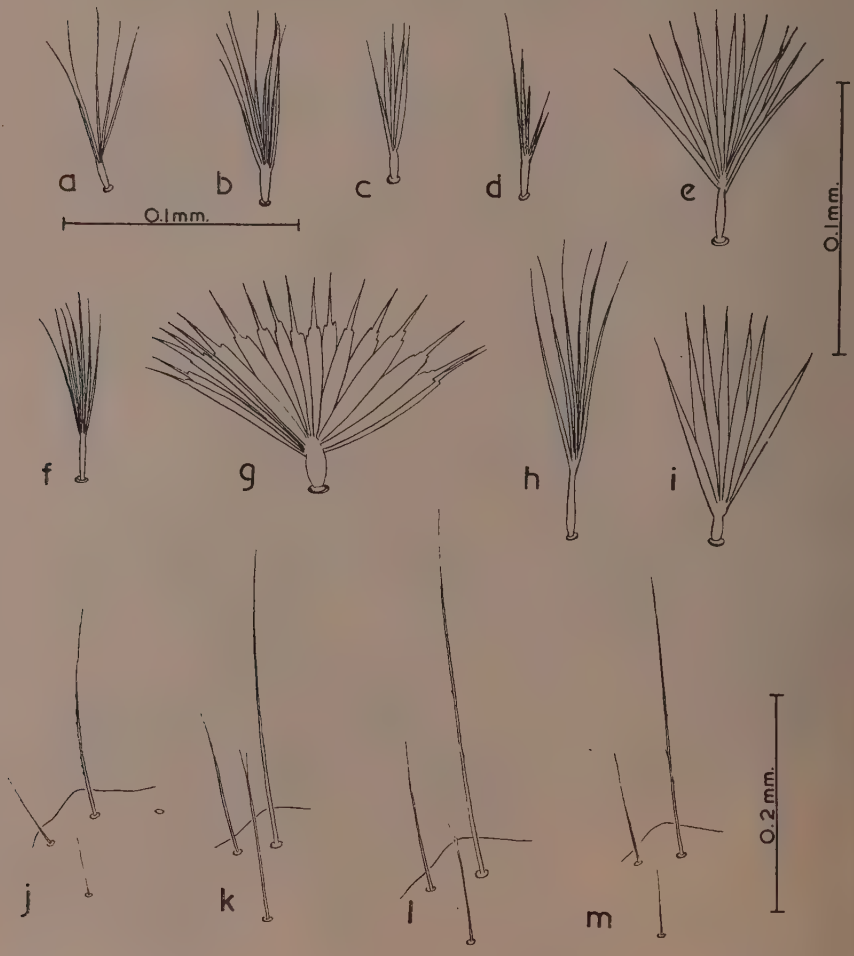

Fig. 4.—*Palmate hairs, abdom. seg. I:* (*a*) "Negros form"; (*b*) *A. l. balabacensis*, Borneo; (*c*) "Luzon form"; (*d*) *A. pujutensis*, Borneo.
Ditto, abdom. seg. II: (*e*) *A. l. balabacensis*, Borneo; (*f*) *A. riparis macarthuri*, Malaya; (*g*) *A. hackeri*, Borneo.
Ditto, metathorax: (*h*) *A. l. balabacensis*, Borneo; (*i*) *A. cristatus.*
Clypeal hairs: (*j*) *A. riparis macarthuri*, Malaya; (*k*) *A. hackeri*, Borneo; (*l*) "Fraser's Hill form"; (*m*) *A. l. balabacensis*, Borneo.

Pupa (fig. 7).

Characterised principally by the long spine IV.A, 0·07–0·08 mm. in length; spine ratios: IV.A/III.A, 3·12–6·00, av. 4·18; IV.A/V.A, 0·67–0·87, av. 0·78 (19 specimens). Side-spicules usually present on spines V.A, VI.A, and VII.A, occasionally on IV.A also Hair II.C brush-like or dendritic, with some 25–30 branches (13–35 in Borneo specimens); hair III.C 7–13-branched, av. 8·6, hair IV.C 5–10-branched, av. 6·4, and hair V.B 5–10-branched, av. 7·1 (40 specimens). T.-M. index 0·82–0·91, av. 0·87 (19 specimens); paddle teeth rather variable in shape but usually moderately coarse.

Larva.

A medium sized larva of medium to pale brown colour, without conspicuous markings.

Head: Antenna length 0·25–0·32, av. 0·29 mm. (70 specimens). *ic* simple or rarely bifid on one side, frequently (23/74) with a few fine side hairs; distance between bases 0·07–0·09, av. 0·084 mm. (38 specimens). *oc* about one-quarter to a third length of *ic* simple. *pc* placed well back, a little external to *ic*., almost always simple; about the same length as *oc* but finer, usually projecting forward to, or past the bases of *ic* (fig. 4).

Thorax: Prothoracic hair 1 of characteristic shape (fig. 3), with strong flattened stem and 10–24 branches, av. 15·6 (70 specimens). The basal tubercles of prothoracic hairs 1 and 2 large, subequal, and partially or entirely fused (49/50); both with a strong, pigmented, apical tooth or spine projecting forward over the base of the hair, this particularly prominent on hair 1 (fig. 3). Prothoracic hair 13 with 4–10 branches, av. 5·8 (70 specimens), almost always (66/70) with 7 or less branches. Metathoracic palmate hair (fig. 4) long and attenuated, showing some differentiation into a basal portion and 2–11 primitive leaflets. All hairs simple in pro- and mesopleural groups; metapleural hair 12 with 1–3 branches, usually 2.

Abdomen: Palmate hairs (fig. 4): Seg. 1, small, with differentiated swollen stem and 5–12 hair-like or flattened branches, almost always with 7 or more on at least one side; seg. 2, moderately developed, with 10–20 leaflets, usually obviously lanceolate, occasionally with slight differentiation of filaments (best seen in unmounted specimens); segs. 3–6, fully developed with 15–23 leaflets, about 0·08 mm. in length, filament somewhat variable but usually quite sharply differentiated and one-third to a half as long as blade; seg. 7 with 9–15 leaflets, usually lanceolate only. Hair I.3 simple or bifid, rarely (4/70) 3-branched on one side only, av. 1·5 (66 specimens). Hair I.9 3–5-branched, usually (70/80) with no more than 4 branches, av. 3·6 (81 specimens). Hair IV.13 with 1–3 long spreading branches, rarely (10/70) 4 on one side only, the hair about 0·20 mm. long, more than half the length of adjacent hair 12. Pecten rather variable but usually with teeth of various graduated lengths.

Egg.

(65 specimens, from North Borneo only, from 4 ovipositions and 3 field collections.)

Of whale back type; length 0·49–0·57, av. 0·526 mm.; breadth including floats 0·18–0·21, av. 0·194 mm.; greatest depth 0·13–0·14, av. 0·133 mm. *Upper surface* narrow, concave antero-posteriorly, dark and finely granulated; sides of deck more or less straight and parallel; breadth 0·03–0·05, av. 0·045 mm.; 3–5 bosses at anterior end; 3–4 at posterior end, these erect and prominent. *Lower surface* dark with silvery polygonal pattern. *Floats* with serrate contour in vertical view, well separated from upper surface; length 0·28–0·36, av. 0·318 mm.: depth 0·07–0·08, av. 0·071 mm.: ridges 14–19, av. 16·4. *Frill* about 0·02 mm. in width, erect, striated, continuous all around upper surface but narrowing abruptly at the ends, where it passes around the outside of the bosses. The egg described from Darjeeling by Iyengar (1938) appears to be of this form.

Geographic Variation.

Certain taxonomic characters of the adult show a marked tendency to vary geographically, as described below. The specimens examined have been grouped

into six geographic units: (*a*) Northern Borneo, (*b*) Northern Malaya (Perlis), (*c*) Assam, (*d*) Burma, (*e*) Southern Philippines (Balabac and Palawan), (*f*) Java.

(1) *Accessory sector pale spot.*—This is the most outstanding instance of geographic variation, since it divides the area of distribution rather neatly into two zones, the eastern islands and the western mainland. In the Philippines, Borneo and Java, the ASP of vein 1 frequently extends on to the costa, while in Malaya, Burma and Assam, it does not extend past the subcosta. The actual proportions of specimens with a costal ASP on one or both wings were: Borneo 61/100, Balabac 1/5, Java 5/7, other areas 0/50. (Russell and Baisas, 1936, give the costal ASP as "sometimes present" in specimens from Balabac and Palawan.)

Within Northern Borneo, the development of the ASP varies geographically as analysed in Table II below.

TABLE II.—*Variation in development of ASP in Bornean specimens.*

		ASP to:		
Locality.	Number examined.	Costa, both wings (%).	Costa, 1 wing only (%).	Subcosta or vein 1 (%).
Labuan Is. . .	50	76	12	12
Mainland, coast .	20	50	20	30
Mainland, interior .	30	43	17	40

The mainland population appears to be reasonably homogeneous, but Labuan specimens show much stronger development of the spot. The difference is highly significant ($\chi^2 = 10{\cdot}3$).

A further point is that occasional specimens from Northern Malaya, Assam, Burma, Indo-China and Java (1/8, 2/8, 2/10, 1/2, and 1/7 respectively) show an additional small pale spot in the basal portion of MD on vein 1 proximal to the ASP. This has not been seen from other areas.

(2) *Wing Apex.*—Bornean and Philippine specimens, both male and female, show an interesting departure from the normal marking of the apical wing fringe. Normally there is a long pale area from before vein 2.2 to past vein 3, but 53 out of 95 Bornean specimens and two out of seven from Balabac, showed some degree of dark scaling in this area. Progressive stages in the development of the character can be seen (fig. 1, *f-h.*): (1) a few dark scales or definite dark spot between veins 2.2 and 3, cutting off normal fringe spots at their apices; (2) as (1), but the dark scaling extended to obliterate the fringe spot at 2.2; (3) further extension of the dark scaling, obliterating the fringe spot at vein 3 also—this very rare, (3/95). Such variants were not seen in numerous specimens from other countries.

As with the development of the ASP, there is a degree of geographic variation within Northern Borneo, as analysed in Table III below: variants are classified according to the greatest degree of development of the character in either wing, and the stages are those described above:

TABLE III.—*Variation in apical wing fringe in Bornean specimens.*

Locality.	Number examined.	Normal (%).	Stage 1. (%).	Stage 2. (%).	Stage 3. (%).
Labuan Is. .	45	51	27	22	0
Mainland .	50	60	8	26	6

Thus in Labuan specimens the variation tends to be developed to a lesser degree than in mainland specimens—stage 1 is far commoner and stage 3 has not been seen. Statistical analysis shows the difference to be significant ($\chi^2 = 9{\cdot}22$).

(3) *Presector dark spot, vein* 1.—The number of pale interruptions in this spot tends to be somewhat higher in specimens from the Asiatic mainland, but the difference is not well-defined. Its length also varies—in Bornean specimens it usually (13/20) corresponds in length with the costal spot, but sometimes extends basally into the PSP level. Specimens from the Asiatic mainland, however, usually (23/28) show some basal extension on one or both wings and in 12 out of 28, the spot extended into the distal half of the HD level (fig. 1, *d*); several specimens from N. Malaya showed the very long spot typical of *A. l. leucosphyrus*. Strangely enough a similar slight extension was seen in four out of five specimens from Balabac and Palawan Is., adjacent to Borneo.

(4) *Propleural setae.*—Specimens from Balabac and Palawan differ from all others in frequently possessing single propleural hairs. In five specimens examined, three had these hairs 1 : 1, and Baisas (1938) gives the frequency distribution in 13 specimens as follows : 7 with 1 : 1, 4 with 1 : 2, 2 with 2 : 2. In 62 specimens from other areas, examined by the writer, the distribution was : 3 with 1 : 1, 5 with 1 : 2, 43 with 2 : 2, 10 with 2 : 3, 1 with 3 : 4. The difference is obviously highly significant. ($\chi^2 = 31{\cdot}8$).

(5) *Relative length of palp.*—As shown in Table IX, Javanese specimens have the palp relatively shorter than in other forms. The palp/proboscis ratios show a highly significant departure from homogeneity ($F = 5{\cdot}67$) due to the low figure for Javanese specimens.

(6) *Palp segment ratios.*—The relative lengths of palp segments 3, 4, and 5, show the same division into eastern and western forms as indicated by wing characters. As shown in Table X, the ratios 3/5, and 3/4, are distinctly lower in specimens from Northern Malaya, Burma and Assam than in those from Borneo and Java. Statistical test of the ratio 3/5, Borneo against Asiatic mainland, shows a highly significant difference ($t = 5{\cdot}12$).

The variation described above appears to be an instance of the well-known phenomenon, geographic subspeciation. Various levels can be seen ; from the broad east–west, or mainland–island, cleavage, shown by a number of characters ; through local forms, such as the southern Philippine with its reduced propleural hairs, to the even more localised variation in wing characters found within Northern Borneo. No doubt lower levels could be demonstrated by careful analysis. Such variation may be reasonably regarded as indicating diversity of genetic constitution amongst the geographically isolated populations, and could in fact be used as a basis for further subdivision of the species. For the present however such a procedure would appear to be pointless.

Identification.

At the species level, identification of the female is simple, by the sub-equal proboscis, palps, and fore-femora, and the presence of pale interruptions in the PSD, vein 1. Subspecific characters are more difficult, but the PSD of vein 1, more or less corresponding in length with that of the costa, is usually characteristic. More difficult to examine, but of considerable use, is the maxillary index, which is usually around 13 in *l. balabacensis*, and 16 or 17 in *l. leucosphyrus*. In

Borneo the presence of a prominent basal pale band on hind tarsal segment 4 is diagnostic and, in Malaya, the absence of a costal ASP is also useful. However, as shown below, there are a number of intermediate populations in Central Malaya in which the adults can only be separated from *balabacensis* by features of the maxillary and pharyngeal teeth—no true *balabacensis*, as defined above, has yet been seen from that area.

The larva is readily identified by the large fused basal tubercles of prothoracic hairs 1 and 2, and particularly by the presence of a prominent apical tooth on the inner tubercle (fig. 3, *j–l.*); also by the usually broad flattened stem of hair 1. For confirmation, or where the tubercles are difficult to see, as in many live specimens, the long, usually two or three branched hair IV.13 is a useful characteristic; also the usual presence of a fairly well-developed palmate hair on abdominal segment II. In Borneo, where larvae of *l. leucosphyrus* tend to have hair IV.13 resembling that of *l. balabacensis*, the 3–4-branched hair I.9 of the latter is diagnostic. In Malaya, at least one intermediate form occurs with a *balabacensis*-like larva, but its prothoracic hair 13, with eight or more branches on at least one side, separates it from *balabacensis* as defined above.

In the pupa, the long spine IV.A and the chaetotaxy are diagnostic.

Notes.

The systematic status of this form has long been in doubt. Its separate identity was first recognised, as the "Balabac *Anopheles* species or variety", in a study of the Philippine Anophelines by Russell and Baisas (1936); in a subsequent paper, Baisas (1936*a*) accorded it varietal status, as "*var. balabacensis*", to separate it from the Luzon form, for which he retained the name *leucosphyrus*. In a subsequent study of the Philippine forms of the *leucosphyrus* group, King and Baisas (1936) allowed the name to lapse and no mention is made of it in their paper, but it was used in a later revision by Baisas (1938). Colless (1948) used the name *A. l. balabacensis* to describe the common form of "*leucosphyrus*" found in North Borneo but in the following year, Reid (1949) showed that the available evidence scarcely warranted retention of its subspecific status and it was allowed to sink once more into synonymy. However, when in 1950 the writer discovered larval characters for the identification of Bornean *leucosphyrus*, these were checked against Malayan material by Mr. Reid, of the Institute for Medical Research, Kuala Lumpur, and were found to correspond with some specimens but not others. He then discovered that there were corresponding adult differences, *i.e.* that Malayan *leucosphyrus* consisted of two distinct forms, and the separate identity of *balabacensis*, and its occurrence in Malaya, were thus finally established. Mr. Reid has very kindly passed all his information on the group, and a considerable number of specimens, to the writer for use in the present study.

On investigation, the differences between *l. balabacensis* and *l. leucosphyrus* prove to be considerable, particularly in the larval and pupal stages; most adults can be placed with ease in the correct group although, in a small percentage, accurate identification is difficult.

The differences are in fact of such a degree that one is tempted to regard the two forms as separate species, particularly since marked geographic variation occurs within both. On present information, however, their ranges of distribu-

tion do not overlap, and intermediate or variant populations have been found in the Malay Peninsula, suggesting that differentiation is well-advanced but not yet complete. For the present, it seems best to regard the two as geographic subspecies, pending further investigations (*see* further discussion, p. 85).

A. l. balabacensis is apparently the most widespread and common member of the group and has been shown by Colless (1950) to be a malaria vector in North Borneo, and probably in other countries.

Distribution[4] (fig. 8).

Specimens have been identified from the following localities:

PHILIPPINES: Balabac, Palawan.

BORNEO: *North Borneo:* Banggi Is., Sandakan, Jesselton, Labuan, Tambunan district, Beaufort, Membakut. *Sarawak*: Miri, Limbang. *Brunei:* Brunei town, Muara, and Tutong roads.

MALAYA: Perlis, Langkawi Is.

JAVA: Soekaboemi, Sudimoro.

SIAM: Chieng Dao and one unspecified locality.

INDO-CHINA: Laos, and one unspecified locality.

BURMA: Shingbwiyang, Kyondaw, and two unspecified localities.

INDIA: Assam (Mikir foothills; Jura, Lebac Cachar), Bengal (Jalpaiguri), Karwa.

A. leucosphyrus leucosphyrus Dönitz, 1901.

Dönitz, W., 1901, *Insekten-Börse* **18**: 37.

Type locality: SUMATRA: Kajoe Tanam.

TYPE: ? Non-existent. Presumed co-type ♀ in British Museum (Natural History). (Reid, 1949.)

The following description is based on specimens from Malaya and Borneo only.

Adult female.

Closely resembles *A. l. balabacensis*, differing as follows:

(1) *Palp* (fig. 2)*:* Relatively short, palp/proboscis ratio 0·80–0·99 (*see* Geographic Variation). The difference is statistical only, but highly significant. Segment length ratios: *3/5*, 2·4–2·8, av. 2·61; *3/4*, 1·6–1·8, av. 1·70 (10 specimens).

(2) *Wing* (fig. 5(*a*))*: PSD, vein 1* considerably longer than in *balabacensis*, extending basally at least to the level of the centre of the costal HD, frequently to the HP level. The spot frequently with 3 or 4 interruptions, range 2–4, av. 2·8 (16 specimens); this is rather uncommon in *balabacensis*. Fork of vein 4 a little distal to fork of vein 2. (*b*) *ASP, vein 1*, usually extending on to costa on at least one wing (28/32).

(3) *Tarsal banding:* Hind tarsal segment IV rarely with a basal pale band—5 out of 32 specimens had such a band and these were very small.

(4) *Pharyngeal teeth:* 14–16 in number, av. 14·9 (10 specimens); rather long, 0·05–0·06, av. 0·053 mm. (9 specimens).

(5) *Maxillary teeth:* 15–18 in number, av. 16·9 (10 specimens).

[4] I have since seen a series (5 females, 2 males, 2 larval skins, in the British Museum and the London School of Hygiene and Tropical Medicine) from Formosa. All are typical *A. l. balabacensis*, and this is presumably the form encountered there by Chow (1949) and others.

Adult male.

Generally similar to the female; terminalia apparently identical with *balabacensis*.

Pupa.

(1) *Hairs III.C and IV.C:* With 3–13, av. 6·4 and 3–8, av. 4·8 branches respectively (21 specimens).

(2) *Hair V.B:* With 4–7 branches, av. 5·1 (21 specimens).

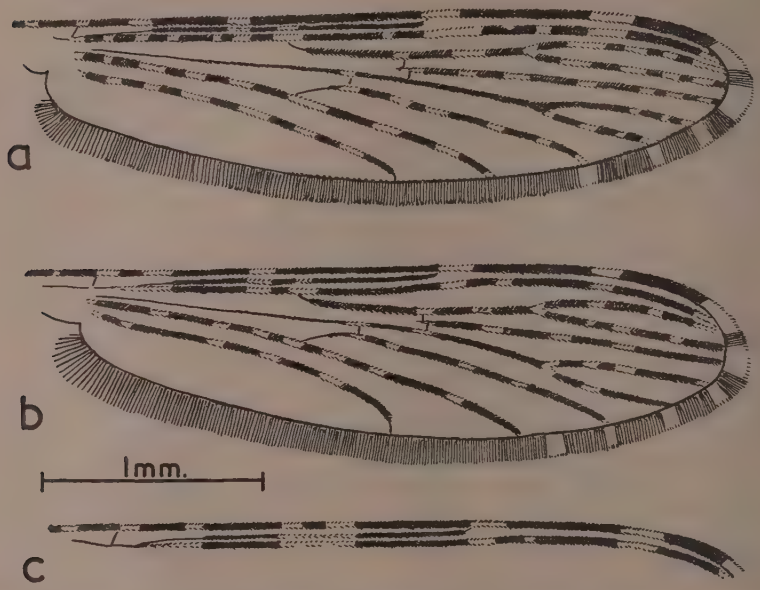

Fig. 5.—*Wings:* (*a*) *A. l. leucosphyrus*, Malaya; (*b*) *A. riparis macarthuri*, Malaya; (*c*) *A. r. riparis*, Mindanao, costa and vein 1.

(3) *Lateral spines* (fig. 7)*:* The length of spine IV.A is rather variable, but clearly shorter than in *balabacensis*; ratios: IV.A/III.A, 1·50–4·00, av. 2·31; IV.A/V.A, 0·21–0·83, av. 0·39 (21 specimens). Spines V.A, VI.A, and VII.A with strong side-spicules.

(4) *Paddle* (fig. 6)*:* Teeth usually rather short and stout, sometimes with a hook-like appearance. Toothed-Margin Index distinctly high, 0·80–0·95, av. 0·90 (21 specimens).

Larva.

(1) *Posterior clypeal hairs:* Rather short, barely reaching level of bases of *ic*.

(2) *Prothoracic hairs 1 and 2:* Much less robust than in *balabacensis*, particularly hair 1, which lacks the broad flattened stem of that species. Also the basal tubercles of both hairs are smaller and well-separated, and that of hair 1 has only a small apical process (fig. 3). This is usually barely visible, but occasionally (1/25) almost as large as in some *balabacensis* specimens.

(3) *Prothoracic hair 13:* With 4–7 branches, av. 6·2 (11 specimens); 6 or more branches present on at least one side (24/25).

(4) *Hair I.9 :* 3–7-branched, av. 5·1 (25 specimens); usually (23/25) with 5 or more branches on at least one side, and rarely (1/25) with as few as 3 branches.

(5) *Palmate hair abdominal seg. II :* Rather variable; leaflets narrowly lanceolate in some specimens, but only about 8–12 in number; generally more weakly developed than in *balabacensis*.

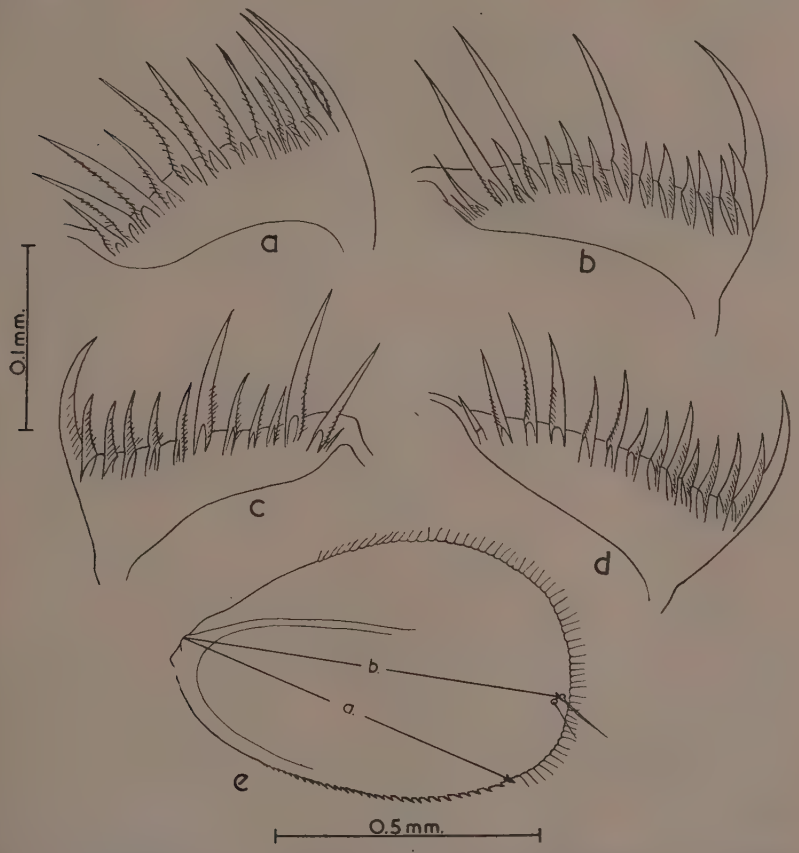

Fig. 6.—*Larval Pecten :* (*a*) *A. cristatus ;* (*b*) *A. l. leucosphyrus*, Malaya ; (*c*) *A. riparis macarthuri*, Malaya ; (*d*) *A. l. balabacensis*, Borneo.
Pupal paddle : (*e*) *A. l. leucosphyrus*, Malaya, showing T.-M. Index measurements.

(6) *Hair IV.13 :* With 2–6 branches, av. 4·1 (23 specimens); 4 or more branches present on at least one side (21/23); the hair fairly short, about 1/3–2/3 the length of adjacent hair 12.

(7) *Pecten* (fig. 6) *:* Usually with well-differentiated long and short teeth.

Geographic variation.

As in the preceding subspecies, several instances of apparent geographic variation have been seen in the specimens examined.

(1) *Relative length of proboscis.*—As shown in Table IX, the proboscis is relatively longer in Malayan specimens than in those from Borneo, as indicated by the palp/proboscis and proboscis/fore femur ratios ; the differences are small but statistically significant ($t = 2{\cdot}32$ and $3{\cdot}46$ respectively).

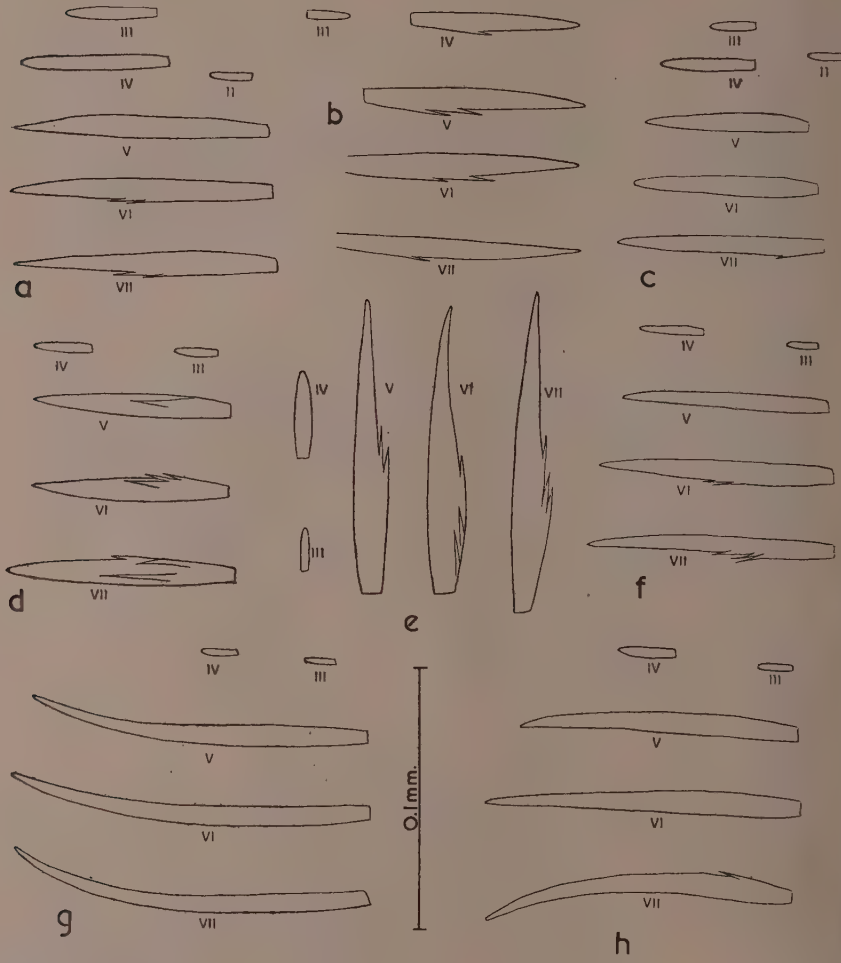

FIG. 7.—*Pupal spines :* (*a*) "Fraser's Hill form" ; (*b*) *A. l. balabacensis,* Borneo ; (*c*) "Negros form" ; (*d*) *A. pujutensis,* Borneo ; (*e*) *A. elegans* ?, W. India ; (*f*) *A. l. leucosphyrus,* Malaya ; (*g*) *A. hackeri,* Borneo ; (*h*) *A. riparis macarthuri,* Malaya.

(2) *Pupal hair III.C.*—As shown in Table XIII, this hair is more highly branched in specimens from Borneo than in those from Malaya ; the difference is statistically significant ($t = 2{\cdot}65$).

Identification.

The adult closely resembles *A. l. balabacensis* and differences are discussed above, under that subspecies. The main diagnostic feature is the long PSD on vein 1, extending basally into the level of the basal half of the costal HD, or further; in Malaya, the presence of a costal ASP and the usual absence of a basal pale band from hind tarsal seg. IV are also useful, but may also be found in some of the intermediate forms mentioned below.

The pupa may be identified by the characters described, the high Toothed-Margin index being its most characteristic feature.

The larva is readily separated from that of *balabacensis* by the weak development of prothoracic hairs 1 and 2 and their basal tubercles, and the rather shorter, and more highly branched, hair IV.13. However, it closely resembles those of *A. pujutensis* and *A. riparis* and occasional misidentification of individual specimens is inevitable. The characters given in Table IV below will, however, give reasonable accuracy, particularly if used with batches rather than single specimens. The figures given are the usual maximum count on either side of the larva.

TABLE IV.—*Identification of larvae of* A. l. leucosphyrus, A. pujutensis *and* A. riparis *in Borneo and Malaya.*

Character.	*A. l. leucosphyrus.*	*A. pujutensis.*	*A. riparis.*
Basal tubercles of shoulder hairs	Separate.	Separate or fused.	Fused.
Prothoracic hair 13 . . .	6 or more.	5 or less.	6 or less.
Hair I.9.	5 ,,	4 ,,	5 or more.
Hair I.3 (Malaya only) . .	2 or less.	2 ,,	3

Notes.

It is assumed above that the forms described from Malaya and Borneo may be identified with the Sumatran type form described by Dönitz (1901). The original type series appears to be no longer in existence, but Reid (1949) has located a presumed co-type in the British Museum, probably the specimen described by Theobald (1901 : 307). Reid's sketch of the wing of this specimen shows the characteristically long PSD on vein 1, and a costal ASP, *i.e.* the diagnostic features of the Malayan form, and so the above identification seems reasonable. However, no Sumatran specimens have been available for thorough study, and further comparison has had to depend on published descriptions and information kindly supplied by Dr. Bonne-Wepster concerning specimens in the Amsterdam Museum.[5]

The lack of larval and pupal specimens from Sumatra is particularly unfortunate, since it is in these stages that many obvious differences are seen between the *leucosphyrus* subspecies. Several "*leucosphyrus*" larvae have been seen from Palembang (*see* p. 82), but these have no corresponding adults, and, in any case, are rather different from any other form seen. The situation obviously requires further investigation.

The distribution of this subspecies poses an interesting problem since, on

[5] I have since been able to examine these specimens, and the cotype, and find them to agree well with the above description.

present information, it is confined to Malaya proper, Sumatra, Sarawak and Indonesian Borneo. A presumable climatic barrier to the dispersal of certain mosquitoes is known to occur in Northern Malaya (Reid, 1950), but the above distribution suggests that a similar situation exists in Borneo also. Much more collecting is obviously needed to trace the actual distribution in that large island, but it is already established that pure populations of what are unmistakably the two forms, *l. leucosphyrus* and *l. balabacensis*, occur in areas only a hundred miles apart. In the western part of the island, *balabacensis* has not been found south of Miri, nor the type form north of that place. There are moreover no obvious differences in terrain, altitude, vegetation, etc., and it is difficult to imagine just what factors could determine this discontinuity. It is hoped that further collecting in the intermediate zone will clarify the situation.

A. l. leucosphyrus is known to be a vector of malaria in Sarawak, and Sumatra (Colless, 1954; Bais, 1920, etc.), but is apparently harmless in Malaya.

Distribution (fig. 8).

Borneo: *Sarawak*: Upper Baram district, Quop, Bidi, Kanowit, Belaga; *Indonesian Borneo*: ? Balikpapan.

Malaya: Selangor, Negri Sembilan.

Sumatra: Kajoe Tanam, Deli, Mandailing.

A. leucosphyrus, " Luzon form ".

Russell, P. F. and Baisas, F. E., 1936, *Philipp. J. Sci.* **59**: 15 (*A.* "*leucosphyrus*," form from Luzon).

Baisas, F. E., 1936, *Philipp. J. Sci.* **59**: 65 (*A.* "*leucosphyrus*" from Luzon).

King, W. V. and Baisas, F. E., 1936, *Proc. ent. Soc. Wash.* **38**: 79 (*A.* "*leucosphyrus*" from Luzon).

Adult female.

Closely resembles *A. l. leucosphyrus*.

(1) *Palp:* Relatively short, palp/proboscis ratio 0·76–0·95, av. 0·87 (4 specimens), segment ratios much the same as in *l. leucosphyrus* (Table X).

(2) *Pharyngeal teeth:* As described and illustrated by Baisas (1936*a*), and confirmed by examination of one specimen, these are of a quite characteristic type—the larger teeth are distinctly shorter and broader than in *l. leucosphyrus*, with deeper, more conspicuous apical fimbriation—length ·034 mm. (1 specimen). They are also fewer in number—about 10 only, while *l. leucosphyrus* has usually about 15.

(3) *Wing:* (a) *The ASP of vein 1* rarely, if ever, extends to the costa—this is implied in the description by Russell and Baisas (1936) of the "Balabac *Anopheles*," and confirmed by my own examination of 6 specimens.

(b) *The PSD of vein 1* is usually but not always long, often extending basally well into the level of the costal HD.

(c) *The PHP of the costa* is rather larger and more conspicuous than is usual in *l. leucosphyrus*.

(d) *The forked cell index*, as given by Baisas (1936*a*) is rather low, 1·23–1·96, av. 1·47 (20 specimens); the fork of vein 2 is frequently a little proximal to fork of vein 4.

(4) *Tarsal banding:* The pale bands of all tarsal segments are reduced and rather inconspicuous, and hind tarsal seg. IV lacks the pale basal band; the bands of the fore tarsi are incomplete beneath, not completely encircling the segments.

Adult male.

Probably differs from *l. leucosphyrus* in number of leaflets on the phallosome. Russell and Baisas (1936) describe the latter as "usually fewer", and their figure shows 7 leaflets on each side, as compared with the usual 8 or 9.

Pupa.

Resembles *A. l. leucosphyrus*.

(1) *Lateral spines :* Baisas (1936*b*) describes spine A of segs. V and VI as "always simple" in the Luzon form. Spine IV.A is also distinctly short; average values for IV.A/III.A and IV.A/V.A, from the data of Baisas (1936*b*) are 1·62 and 0·32 respectively.

(2) *Hair V.B :* Baisas (*op. cit.*) gives 3–5 branches, av. 4·2; this is the lowest average recorded for the group.

(3) *Paddle :* Measurements of 2 specimens, and the illustration by Baisas (1936*a*), give a Toothed-Margin index of 0·75–0·79, av. 0·77, much lower than in *l. leucosphyrus*.

Larva.

Resembles *A. l. balabacensis*.

(1) *Antenna length :* 0·27–0·32, av. 0·288 mm. (8 specimens).

(2) *Posterior clypeal hairs* reaching to, or a little short of, the level of the base of *ic*; usually (6/9) with 2 branches on at least one side.

(3) *Prothoracic hair 1 :* The basal tubercle (fig. 3) has a prominent apical process, as in *balabacensis*, but broader and more rounded at the tip than is usual in the latter form.

(4) *Abdominal palmate hair, seg. II :* Very poorly developed, with a narrow attenuated stem, and 1–12 fine, barely flattened branches.

(5) *Pecten :* The teeth are clearly differentiated into short and long types, the former about half as long as the latter.

Identification.

As far as is known this form is restricted to Luzon, and is the only one occurring there. Its principal identifying features are: in the adult, the tarsal banding; in the pupa, the three points given above; in the larva, the abdominal palmate hair on seg. II and the pecten.

Notes.

This form has long been recognised as distinct from others occurring in the Philippines, but its relationship to those of other countries has remained doubtful and the above authors have provisionally identified it with the type form. It was pointed out by Colless (1948) that this was probably incorrect, and now that it has been possible to make a more detailed comparison, it is obvious that the "Luzon form" is a distinct geographic form of *A. leucosphyrus*.

Its systematic status is rather perplexing, since in all three stages it falls in a position more or less intermediate between *l. leucosphyrus* and *l. balabacensis*; the adult and pupa tend to resemble the former and the larva, the latter, while the shape of the pharyngeal teeth is quite different from that found in any other form of "*leucosphyrus*". Its distribution suggests derivation from *l. balabacensis* by colonisation across the Palawan-Mindoro zoo-geographic boundary, but if this is so, its resemblance to *l. leucosphyrus* must be coincidental, by convergence. It is perhaps best to regard it as a distinct subspecies, the direct descendant of an ancestral form which penetrated to Luzon prior to the differentiation of the present subspecies.

The formal recognition of this form, as subspecies or species, will have to be left to the judgement of those workers in the Philippines who first established its separate identity and who have a sufficient supply of specimens.

Distribution (fig. 8).

Known only from PHILIPPINES : Luzon.

A. leucosphyrus, " Fraser's Hill form "

A number of Malayan specimens have been seen which, while obviously belonging to *A. leucosphyrus*, appear to form a homogeneous group not identifiable with any of the preceding subspecies. Most are from Fraser's Hill, Pahang (7 ♀, 10 larval and pupal skins), with a further two females from other areas in Central Malaya. There is a distinct resemblance to *A. l. balabacensis*, but also some marked differences ; the principal characteristics are given below.

Adult female.

Head (See Tables IX and X) : Proboscis/fore femur and palp segment ratios close to those for Malayan *l. leucosphyrus* but palp/proboscis ratio as in the Bornean form, and *l. balabacensis*. Pharyngeal teeth (fig. 2) rather long and noticably thin and numerous, 16–20 in number, av. 17·3 (6 specimens). Maxillary teeth 16–18, av. 17·2 (6 specimens).

Wing (fig. 1) *:* of the *balabacensis* type, with PSD, vein 1, corresponding in length with that on the costa ; the spot with no more than 1 pale interruption and, in 4/9 specimens, undivided on one wing ; ASP small, shorter than basal portion of MD, and not extending to costa.

Legs : Hind tarsal seg. IV with a small to minute basal pale band (5/9) or none (4/9).

Pupa.

Spine IV.A only moderately long, relative length much the same as in *l. leucosphyrus* (Table XIV). Hairs III.C and IV.C rather strongly branched ; T.-M. index close to that of *l. balabacensis* (Table XIII).

Larva.

Closely resembles that of *l. balabacensis*, but noticeably larger ; antenna length 0·32–0·35, av. 0·33 mm. (10 specimens). *pc.* reaching to, or past, anterior margin of the head, simple or (2/10) bifid at the tip. Prothoracic hair 1 with 15–23 branches, av. 18·8 ; prothoracic hair 13 with 6–10, av. 8·3, with 8 or more branches on at least one side ; hair I.9 3–6 branched, av. 4·6 (10 specimens in each case) ; hair IV.13 with 3 long branches or 4 branches on one side only (1/10). The large size is possibly correlated with altitude since the larvae were collected at approximately 4000 ft.

Notes.

The obvious affinity of this form with *l. balabacensis* suggests that it should be regarded as the Central Malayan representative of that subspecies. It possesses, however, some very characteristic taxonomic features : in the adult, the reduced subdivision of PSD, vein 1, and the reduced basal pale band of hind tarsal seg. IV, the long and numerous pharyngeal teeth and the high maxillary index ; in the pupa, the rather short spine IV.A and few branches to hair V.B, associated with features otherwise resembling *balabacensis ;* in the larva, the highly branched prothoracic hairs 1 and 13, and hair I.9. It is noticeable that in

some of these characters there is a resemblance to *l. leucosphyrus*. The situation is further complicated by the fact that the " Fraser's Hill form " is found in Central Malaya along with the latter subspecies and that there is found there yet another, apparently distinct, *balabacensis*-like form (*see below*). These facts suggest that in Central Malaya, where the ranges of *l. leucosphyrus* and *l. balabacensis* meet, hybridisation has produced a zone of secondary intergradation in which occur a number of intermediate forms. For the present then, such presumed hybrids are described under vernacular names, pending further investigations.

Distribution (fig. 8).

MALAYA : Pahang (Fraser's Hill) ; N. Sembilan (Kg. Inas).

A. leucosphyrus, " Kepong form "

? " *A. leucosphyrus*, " long spine IV " type, of Crawford (1938).

A second series of Malayan specimens (5 ♀, 2 ♂, 6 larval and pupal skins) found in the collection of this Department, also exhibits characters intermediate between the type-form and *l. balabacensis*, but is quite distinct from the " Fraser's Hill form ". These specimens have, unfortunately, no locality labels, but appear to be from a single locality, probably in Central Malaya. Two other females from Kepong, Selangor, resemble these closely and the whole series is here treated as a separate intermediate form with the characters described below.

Adult female.

Head (See Tables IX and X) : Proboscis, palp, and fore femur ratios much the same as in *l. balabacensis* and the Fraser's Hill form. Palp segment ratios as in the mainland forms of *l. balabacensis*. Pharyngeal and maxillary teeth as in the type form.

Wing : of the normal *balabacensis* type ; PSD, vein 1, corresponding in length with that on the costa, or extending a little basally, with 1–3 pale interruptions. ASP extending to costa on at least one wing in 5/7 specimens, otherwise to the subcosta. Basal portion of MD, vein 1, with an additional pale interruption, proximal to the ASP, in 4/7 specimens.

Leg : Hind tarsal seg. IV without any basal pale band.

Pupa (6 specimens).

Spine IV.A long, av. length 0·064 mm. Spine III.A also quite long, av. 0·027 mm., the longest for the whole group. Ratio IV.A/III.A therefore rather low, of the *l. leucosphyrus* type, but IV.A/V.A of the *balabacensis* type (Table XIV). Spine IV.A with side-spicules in several specimens. Hairs III.C, IV.C, and V.B all strongly branched (Table XIII). T.-M. index high, 0·89–0·94, av. 0·92.

Larva (6 specimens).

Head : pc. rather long, reaching to, or almost to, anterior margin of the head, simple or (2/6) bifid at the tip.

Thorax : Prothoracic hair 1 with 11–21 branches, av. 13·9 ; the basal tubercle with a distinct apical projection, as in *balabacensis*, but in 5 out of 6 specimens, distinctly weaker and more rounded than is usual in the latter form. Prothoracic hair 13 with 6–10 branches av. 7·6, at least one side with 7 or more branches.

Abdomen : Hair I.3 with 2–4 branches, av. 2·9, at least one side with 3 or more branches. Hair I.9 with 5–6 branches, av. 5·0. Hair IV.13 3- or 4-branched, av. 3·8,

with 4 branches on at least one side ; the hair fairly short, about half the length of adjacent hair 12. Palmate hair on seg. II weakly lanceolate.

Notes.

This form, like the preceding, shows a marked resemblance to *l. balabacensis*, but possesses features which make it difficult to include it under that subspecies. In the adult the presence of a costal ASP and absence of the basal pale band on hind tarsal seg. IV, and the number of pharyngeal and maxillary teeth, are all typical of *l. leucosphyrus*. In the pupa, the spine length ratios are rather intermediate, but spine III.A is quite remarkably long (in absolute length) ; hairs III.C, IV.C and V.B are rather more strongly branched than in most *balabacensis*, but the T.-M. index shows the high value typical of *l. leucosphyrus*. The larva shows a general resemblance to that of the " Fraser's Hill form ", but hair IV.13 resembles that of *l. leucosphyrus*, and the highly-branched hair I.3 appears to be peculiar to this form alone.

[6]For the present, then, it seems best to treat this form as another intermediate, occurring in a zone of hybridisation at the junction of the ranges of the type-form and *balabacensis*. The pupal spine-lengths and ratios, and the branching of hair V.B suggest that this was the " long spine IV " type of *A. leucosphyrus*, described by Crawford (1938).

Distribution (fig. 8).

Malaya : Kepong Forest Reserve (Selangor), and one unspecified locality.

A. leucosphyrus, " Negros form "

A small series of specimens from the Philippine island of Negros possesses a number of distinctive characters which appear to warrant description as a separate form. As in the two preceding forms, there is a general resemblance to *A. l. balabacensis*.

Adult Female (2 specimens).

Palp/proboscis ratio 1·00, proboscis/fore femur ratio 0·93 (1 specimen). Wing of *balabacensis* type, with 1 interruption in PSD, vein 1, and the ASP extending to the costa. Hind leg with very small basal pale patch on tarsal seg. IV.

Pupa (3 specimens) (fig. 7).

Spine lengths and ratios much the same as in the " Fraser's Hill form," though spine V.A rather shorter (Table XIV). Hairs III.C, IV.C and V.B rather weakly branched, resembling those of the " Luzon form," as does the very low T.-M. index.

Larva (3 specimens).

Resembles *balabacensis*, but rather large—antenna length 0·30–0·31, av. 0·31 mm. Hair I.9 with 3–5 branches, av. 4·7, at least one side with 5 branches. Hair 1 on

[6] I have recently received a series of what appears to be this form, taken biting in jungle by the U.S. Army Medical Research Unit, Kuala Lumpur. The same catches also contained fair numbers of *l. leucosphyrus* and I can now see no reason for regarding the two forms as other than specifically distinct. It seems likely that further revision of the nomenclature will be needed to raise *balabacensis* to specific rank and then to include the " Kepong " and the " Fraser's Hill " forms among its subspecies.

metathorax and abdominal seg. II not palmate, hair-like, with 2–6 and 4–5 branches respectively (fig. 4).

Notes.

Only a few specimens of this form have been seen, but despite its general resemblance to *l. balabacensis*, its larval and pupal characters prevent its inclusion under that subspecies as defined in this paper ; the weak development of the larval palmate hairs is particularly striking. In all stages there are points of resemblance to the " Luzon form ", suggesting that we have here a local form transitional between that subspecies and *balabacensis*—its distribution also

Fig. 8.—Tentative map of distribution of forms of *A. leucosphyrus* sens. strict. Broken line = *A. l. leucosphyrus* ; dotted line = *A. l. balabacensis** ; stippled areas : *1*, Formosan *A.* " *leucosphyrus*"* ; *2*, the " Luzon form " ; *3*, the " Negros form " ; *4*, the " Fraser's Hill form " and " Kepong form."

* See footnote on p. 55.

agrees with such a view. The actual position can only be settled by further collecting.

Distribution (fig. 8).

Philippines : Negros Is.

A. riparis riparis King and Baisas (1936)

King, W. V., and Baisas, F. E., 1936, *Proc. ent. Soc. Wash.* **38** : 79. (*A. leucosphyrus* var. *riparis*.)

Type locality : Mindanao : Kolambugan.

Types : Female and male with larval skins, in the U.S. National Museum.

The following description is based on that of King and Baisas (1936), and a more detailed examination of three females and 10 larvae, from the collection of the Department of Health, Manila.

Adult female

Head : Palps with rather thick, " stubby " appearance, due to the relative shortness of segs. 4 and 5 ; segment ratios : *3* 5–3·09, *3/4*–1·89 (1 specimen). Palpal banding rather variable ; bands usually narrow and seg. 5 merely tipped with white, but some specimens with broader bands—King and Baisas (*op. cit.*) record two with segs. 4 and 5 largely pale. Pharyngeal teeth about 10 in number, of characteristic shape, rather stout but

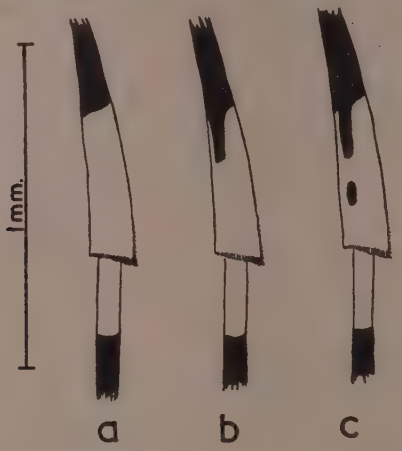

Fig. 9.—*Hind-leg, tibio-tarsal band* (semi-diagrammatic). (*a*) *A. l. balabacensis*, Borneo ; (*b*) *A. riparis macarthuri*, Malaya ; (*c*) " Celebes form."

tapering, with the tips not very deeply indented. Maxillary index very high, 20 : 21 (1 specimen).

Thorax : Propleural setae single.

Wing (fig. 5) *:* Costa with PHP and usually with prominent ASP. Vein 1 with PSD complete, without pale interruptions, about as long as that on the costa ; ASP prominent, much longer than the basal stub of MD and not infrequently continuous with SP, *i.e.* the basal stub absent ; PAD with 1 pale interruption or, rarely, none. Base of *pf* often proximal to base of *af*.

Legs : Fore femur relatively long ; ratio proboscis/fore femur 0·87–0·92, av. 0·89, palp fore femur 0·81–0·89, av. 0·86 (3 specimens). Broad apical pale band of hind tibia divided on at least the basal half of its ventral aspect by a linear stripe of dark scaling (fig. 9). First tarsal segments well-speckled, that of mid-leg with up to 15 spots, average about 6. Tarsal banding reduced, more or less absent from mid-legs ; the hind tarsal seg. IV without a basal pale band.

Abdomen : Seg. VII without any ventral tuft of dark scales.

Adult male.

Generally similar to female. Terminalia resembling those of *balabacensis*, but leaflets of phallosome possibly a little shorter ; King and Baisas (*op. cit.*) give the length as 0·035–0·040 mm.

Pupa.

Unknown.

Larva.

Rather closely resembles that of *balabacensis*, differing as follows :

(1) *Posterior clypeal hairs :* 1–3-branched, av. 1·7 (10 specimens), usually with 2 or more branches on at least one side (9/10) ; (King and Baisas (1936) give " usually simple, sometimes 2–5-branched ").

(2) *Prothoracic hair 1 :* With basal tubercle less strongly developed : without any prominent apical tooth, but usually with a small but obvious rounded projection (fig. 3).

(3) *Abdominal palmate hair, seg. II :* Partially developed, with flattened branches or clear lanceolate leaflets, but obviously weaker than in most *balabacensis*.

(4) *Hair I.9:* With 4–6 branches, av. 5·1 (9 specimens), at least one side with 5 or more branches (9/9). Hair 9 on segs. III, IV, and V also more strongly branched.

(5) *Hair II.13:* With 5–10 branches, av. 7·1 (9 specimens) ; at least one side with 6 or more branches (9/9).

(6) *Lateral hairs of segs. IV and V:* Commonly 3-branched on at least one side (6/9).

(7) *Pecten :* Tends to resemble that of the " Luzon form," rather than *balabacensis*, but rather intermediate.

Identification.

The principal diagnostic characters of the adult female are : (1) the undivided PSD on vein 1 and presence of only one interruption in PAD ; (2) the subequal palp and proboscis ; (3) the line of dark scales in the tibio-tarsal band. The presence of a costal PHP and the shape of the pharyngeal teeth distinguishes the species from *A. cristatus*, while differences from *riparis macarthuri* are discussed under that form.

The larva is fairly distinct and unlikely to be confused with any but *balabacensis* and the " Luzon form " ; the form of the basal tubercle of prothoracic hair 1 and the branching of hair I.9 should give complete separation from these.

Notes.

Although originally described as a " variety ", *A. riparis* is morphologically distinct from all other members of the group and shows sympatric distribution with some of them, making it obvious that it is, in fact, a good species. Its rather peculiar distribution is discussed under the next subspecies.

Distribution (fig. 11).

Philippine Islands : Mindanao, Negros.

A. riparis **macarthuri** subsp. n.

A. leucosphyrus, " short spine IV " type, Crawford (1938).

Type locality : Sarawak : Long Tebangan, 4th Division.

Types : Holotype female, allotype male, male and female paratypes, all with corresponding larval and pupal skins, in the British Museum (Nat. Hist.).

Adult female.

Closely resembles *riparis riparis* but rather larger and differing as follows :

(1) *Palps :* With relatively broader pale bands, seg. 5 pale on at least the apical half ; segment 5 relatively short as in *r. riparis* (Table X).

(2) *Wing* (fig. 5) *:* PHP occasionally missing from costa (4/42). ASP of vein 1 smaller, usually (36/42) of approximately the same length as the basal stub of MD, rarely (2/24) continuous with SP on one wing only ; ASP rarely (7/54) extending on to costa of either wing—Reid (1949) gives 7/20 for Malayan specimens.

(3) *Legs :* Mid tarsal seg. 1 with 0–4 pale spots, not conspicuously speckled. Fore femur relatively shorter ; ratios, proboscis/fore femur 0·88–1·03, av. 0·95, palp/fore femur 0·82–0·98, av. 0·88 (27 specimens).

(4) *Propleural hairs :* Commonly double on one or both sides. (*See* Geographic Variation.)

(5) *Pharyngeal teeth* (fig. 2) : 10–13 in number, stout and short, deeply dissected at apices ; length 0·035–0·042, av. 0·039 mm. (9 specimens).

Adult male.

Generally similar to the female, but costal ASP more commonly present on one or both wings (21/25). ASP on vein 1 rather larger. Frequently with 2 or 3 propleural hairs on one or both sides (20/25).

Pupa (fig. 7).

Characteristic features are :

(1) *Hair II.C :* With only 10–22 branches, av. 15·4 (20 specimens).

(2) *Spine IV.A :* Very short ; ratios IV.A/III.A and IV.A/V.A are 1·00–4·00, av. 1·79, and 0·11–0·27, av. 0·18, resp. (20 specimens).

(3) *Hair V.B :* With 4–10 branches, av. 6·3 (26 specimens) ; usually at least one side 6 or more branches (21/26), frequently with 7 or more (14/26).

(4) *Paddle teeth :* Somewhat finer than in other forms ; Toothed-Margin Index rather low, 0·71–0·84, av. 0·79 (20 specimens).

Larva.

Tends to resemble that of *l. leucosphyrus* or *pujutensis*, rather than that of *r. riparis*, although there are distinct resemblances to the latter form. Characteristic features are :

(1) *ic :* Usually with fine side hairs on the central third, these rather more numerous than in other forms (fig. 4).

(2) *pc :* Rarely bifid (2/30), and only just reaching to the level of the bases of *ic*.

(3) *Prothoracic hairs* 1 *and* 2*:* With moderately strong development of the basal tubercles; these usually fused on one or both sides (27/30), and with a fairly prominent, rounded, apical process on the inner tubercle ; a " lip " rather than a " tooth " (fig. 3).

(4) *Abdominal palmate hair on seg. II :* Very weakly developed, with differentiated stem but barely flattened branches (fig. 4).

(5) *Hair* I.9 *:* With 5 or more branches on at least one side (32/33), usually (29/33) on both.

(6) *Hair IV*.13 *:* With 4 or more branches on at least one side (30/32), the hair short, about half the length of adjacent hair 12. (*See* Geographical Variation.)

(7) *Lateral hairs on seg. IV:* Usually (24/31) 3-branched on at least one side ; rarely so (8/29) on seg. V.

(8) *Pecten :* As in *r. riparis* (fig. 6).

Geographic variation.

Specimens from Malaya and Sarawak differ markedly in several adult and larval characters, as described below.

Adult.—The proportion of specimens possessing doubled propleural hairs is much higher in Bornean specimens than in those from most parts of Malaya, with the exception of a small batch from Cameron Highlands. *See* Table V below :

TABLE V.—*Frequency distribution of propleural hairs in* A. riparis macarthuri.

Specimens.		Number.	Propleural hairs. 1 : 1	1 : 2	2 : 2	2 : 3	3 : 3
Malaya—Cameron Highlands,	♀	9	2	2	5	0	0
„ — „ „	♂	6	2	1	1	2	0
„ —Other areas,	♀	20	15	3	2	0	0
„ — „ „	♂	6	2	2	2	0	0
Sarawak	♀	18	0	1	11	6	0
„	♂	10	0	0	7	2	1

Within Malaya, females from Cameron Highlands have two hairs on one or both sides in the majority of specimens, while the condition is infrequent in those from other areas (including almost every state of the Federation, and Singapore). The difference is statistically significant ($\chi^2 = 8{\cdot}49$). In females from Sarawak, doubled hairs are even more common than in those from Cameron Highlands, and the 2 : 3 condition is common. In males much the same variation is found, though differences within Malaya are less marked.

Larva.—Two larval hairs, I.3 and IV.13, and larval coloration, also show significant variation.

(a) *Hair I.3* : In Malayan larvae this hair is commonly three-branched on at least one side (18/20) and the unbranched condition is rare (2/20). In larvae from Sarawak, the three-branched condition is uncommon (4/12, on one side only), while the hair is often simple (5/12).

(b) *Hair IV.13 :* In Malaya, this hair has five branches on at least one side, and usually (16/20) on both ; none were seen with less than four branches. In Sarawak, the five-branched condition is rare (2/12, on one side only), while three branches are usual on one or both sides (10/12). Corresponding with the greater degree of branching, the hair is also a little shorter in Malayan specimens.

(c) In live specimens, larvae from Sarawak frequently show a striking pattern of pale transverse bands or spots on the thorax and abdomen, in much the same fashion as the larva of *A. hackeri.* Mr. Reid informs me that such markings are never seen in Malayan specimens.

Identification.

The adult possesses the specific characters described under *A. riparis riparis*, but differs from that subspecies in the usual absence of a costal ASP, the reduced speckling of mid tarsal seg. 1, and the shape of the pharyngeal teeth ; also the tendency to possess two or more propleural hairs.

The pupa may be identified with a fair degree of accuracy by the short spine IV.A, the low T.-M. index, and the weakly-branched hair II.C.

In the larval stage Malayan specimens are clearly separated from the Philippine subspecies by the characters of hairs I.3 and IV.13, but Bornean specimens are less distinct. Table IV (p. 59) summarises differences from the closely similar *l. leucosphyrus* and *pujutensis.*

Notes.

Although this form is separated from the Philippine subspecies by differences which are mostly of a statistical nature, the magnitude of such differences and the marked geographic separation appear sufficient to warrant its formal recognition as a separate subspecies. The differences found between the Bornean and Malayan forms are a complicating factor, but further subdivision seems unwarranted and the two are sufficiently alike for inclusion under a single subspecies.

Though present records are rather inadequate, it seems likely that *riparis macarthuri* has essentially the same distribution as *l. leucosphyrus*, confined to the Malay Peninsula and the southern half of Borneo, and reappearing as an allied subspecies in the southern Philippines. It seems probable that the same limiting factors (? climatic) determine the distribution of both.

Distribution (fig. 11).

Malaya : numerous localities throughout the Peninsula and Singapore.
Borneo : Sarawak (Akah River).

A. cristatus King and Baisas (1936).

King, W. V. and Baisas, F. E., 1936, *Proc. ent. Soc. Wash.* **38** : 79.

Type locality : Mindanao : Titunod, Kolambugan.

Types : Female and male, with larval and pupal skins, in the U.S. National Museum.

The following description is based on the original by King and Baisas, supplemented by examination of a number of specimens from the Department of Health, Manila.

Adult female.

Closely resembles *A. riparis riparis*, its characteristic features being as follows :

(1) *Head :* Palps with very narrow pale bands, the apical segment usually merely tipped with white ; segs. 4 and 5 relatively short as in *riparis* (Table X). Maxillary index similarly high, 21 : 22 (1 specimen).

(2) *Propleural hairs :* Single.

(3) *Wing :* Costa usually without PHP (14/16, King and Baisas, *op. cit.*), and frequently with ASP (3/4). Vein 1 with PSD undivided ; MD with at most one pale interruption, the ASP, which is large and prominent and usually (4/4), continuous with the SP ; PAD with one pale interruption or none. Base of *af* proximal to base of *pf*.

(4) *Legs :* Fore femur relatively longer than in all other forms ; palp/fore femur ratio 0·77–0·86, av. 0·82, proboscis/fore femur 0·85–0·90, av. 0·87 (5 specimens). Tarsal bands reduced, barely apparent on mid-leg ; first segment of mid-tarsi unspeckled or with up to 4 pale spots ; hind tarsal seg. 4 without basal pale band. Apical pale band of hind tibia with a dark stripe on ventral aspect.

(5) *Abdomen :* Without a ventral tuft on seg. VII.

Adult male.

Generally similar to female. Phallosome with 5–9 leaflets per side, these rather short (length of longest leaflet 0·030–0·035 mm., according to King and Baisas) and sparsely serrated.

Pupa.

Characteristic features (from Baisas, 1936*a*): hair II.C with 7–16 branches, generally arranged in one plane, like a fan; hair C of segs. III and IV with 6–17, av. 8·7, and 3–8, av. 5·3, branches respectively. Hair V.B with 6–11 branches, av. 8·7. Spine IV.A relatively short, ratios IV.A/III.A and IV.A/V.A being about 1·3 and 0·2 respectively. Spines V.A, VI.A, and VII.A usually with side-spicules.

Larva.

Head: *ic* stout basally with side branches on basal half; *oc* stout with several stout side-branches; *pc* of extremely characteristic appearance, long, reaching well past anterior margin of the head, and conspicuously branched along a stout stem. The bases of *ic*, *oc*, and *pc* on one side form an approximately equilateral triangle.

Thorax: Prothoracic hair 1 with 14–20 branches, av. 16·5 (10 specimens); the basal tubercle relatively weak, with an inconspicuous apical process, not fused with tubercle of hair 2. Prothoracic hair 13 with 6–10 branches, av. 8·4 (10 specimens) usually (8/10) with 8 or more branches on at least one side. Metathoracic palmate hair fairly well developed, more so than in any other member of the group, with 6–12 sharply tapering leaflets (fig. 4).

Abdomen: Palmate hairs: on seg. I, rudimentary, with 2–6 flattened branches, of markedly different lengths; on seg. II, fully developed with 11–24 fully differentiated leaflets, similar to, but rather smaller than, those on following segments; leaflets on remaining segments with sharply differentiated fine-pointed filaments. Hair II.13 usually 3-branched, conspicuously long and strong. Hair IV.13 as long as, or longer than, hair IV.12 and markedly stronger, with 2 or 3 branches (usually 3). Lateral hairs: on seg. III, with relatively few branches, 6–14, av. 9·2; on seg. IV, 3–5-branched, av. 3·5; on seg. V, 2–4-branched, av. 2·9 (all 10 specimens).

Identification.

The adult characters readily separate *cristatus* from all others but *riparis*, from which it may usually be distinguished by the absence of the PHP. The fore femur of *cristatus* is also rather longer and the pharyngeal teeth have a very characteristic shape.

The pupa is apparently characterised by its short spine IV.A and the branching and shape of hair II.C, but it is possible that, in these, it resembles the still unknown pupa of *riparis riparis*. However, the presence of side-spicules on the lateral spines and the branching of hairs III.C and V.B are probably characteristic.

The larva is immediately identifiable by a number of prominent characters; the form of the posterior clypeal hairs alone distinguishes it from all other Oriental Anophelines.

Notes.

This rare species is almost certainly an off-shoot of the *riparis* stock and probably arose, during geographic isolation, from an early *riparis*-like colonist of Mindanao. The larval differences between *riparis* and *cristatus* are striking, but are paralleled by those in other forms, *e.g.* between the obviously related *A. watsoni* and *A. stookesi*.

A. cristatus has a very limited distribution on the island of Mindanao and Baisas (1936*a*) records the probability of its rapid extinction through deforestation.

Distribution (fig. 11).

Known only from the type locality.

Note : Van Hell (1953) records the larva of this, or a closely similar species, from New Guinea ; until adults are available, however, the record must remain doubtful.

A. pujutensis Colless (1948).

Colless, D. H., 1948, *Proc. linn. Soc. N.S.W.* **73** : 101. (*A. leucosphyrus pujutensis.*)

Type locality : SARAWAK : Pujut.

Types : Type series (males, females, and larvae) in the C.S.I.R.O. Museum, Canberra, Australia. Paratypes in the British Museum (Nat. Hist.).

Synonyms. A. leucosphyrus var. *hackeri*, Edwards (1921), *in part.*

Adult female.

Head (fig. 2): Proboscis long, 1·9–2·5, av. 2·3 mm. (15 specimens), ratio proboscis/fore femur 1·24–1·38, av. 1·29 (15 specimens) ; a narrow ring or " tache " of golden scales present at the apex behind the labella. Palps distinctly shorter than proboscis, but judged by absolute size, rather long (*See* Table VIII) ; ratio palp/proboscis 0·72–0·87, av. 0·83 ; palp/fore femur 0·95–1·15, av. 1·06 (15 specimens) ; palpal banding normal, apical pale band and preapical dark band of about the same length ; segment ratios much the same as in *l. leucosphyrus*. Pharyngeal teeth resemble those of *A. l. balabacensis*. Maxillary index 14–19 (*see* Geographic Variation).

Thorax : Propleural setae 1–4, av. 2·5 (42 specimens). (*See* further details under Geographic Variation).

Wing (fig. 10) : PHP of costa always small, frequently minute, occasionally (4/15) absent. ASP of vein 1 large and prominent, markedly longer than basal stub of MD, often (27/40) extending on to the costa of at least one wing. Vein 1 with PSD undivided, corresponding in length with the costal spot ; MD with 1–3 pale interruptions, usually (13/15) with 2 or more on at least one wing ; PAD similar, usually (14/15) with 2 or more interruptions. The apical wing fringe resembles that of Borneo and Philippine *balabacensis*, in that some specimens show dark scaling in the pale area between the apices of veins 2·2 and 3. (*See under* Geographic Variation.) Rarely (1/41), a small pale interruption is found in MD of the costa, distal to the ASP. Forked cell index 1·5–1·7, av. 1·63 (20 specimens). Base of *af* proximal to base of *pf*.

Legs : Similar to those of *balabacensis*, but usually lacking the pale basal band on hind tarsal seg. 4 : of 25 specimens examined, 6 had a very small to minute pale dorsal patch in this position.

Adult male.

Generally similar to female. Wing with dark areas reduced ; ASP almost always (14/15) present on costa. Propleural hairs 1–3, usually (12/15) with 2 on at least one side. Terminalia apparently identical with those of *balabacensis*.

Pupa (fig. 7).

Characteristic features are :

(1) *Hair II.C :* With some 20–30 branches, as in *balabacensis*.

(2) *Hairs III.C. and IV.C :* With relatively few branches—4–10, av. 6·0, and 3–6, av. 4·4, respectively (18 specimens).

(3) *Hair V.B:* With 3–6 branches, av. 4·8 (18 specimens), usually (13/18) with no more than 5 branches.

(4) *Spine IV.A:* Relatively short; ratios IV.A/III.A and IV.A/V.A are 1·00–1·80, av. 1·53, and 0·18–0·40, av. 0·28, respectively (18 specimens).

(5) *Terminal paddle hair:* Often rather stout with a characteristic curved or hook-like appearance.

(6) *Paddle teeth:* Rather stouter and coarser than in other forms. Toothed-Margin Index 0·76–0·87, av. 0·83 (18 specimens).

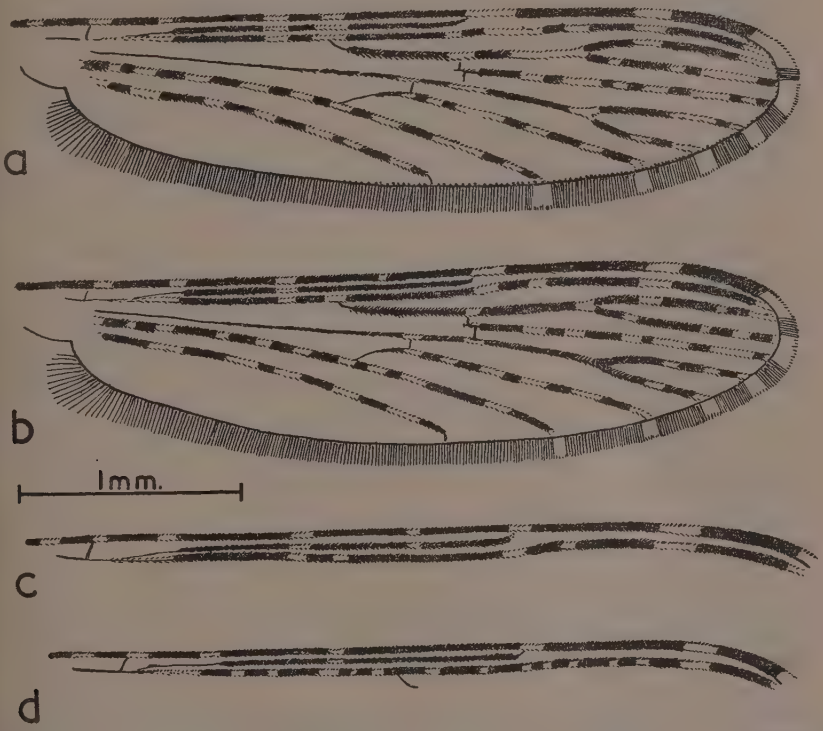

Fig. 10.—*Wings:* (*a*) *A. pujutensis*, Borneo; (*b*) *A. hackeri*, Borneo; (*c*) *A. elegans* Ceylon, costa and vein 1; (*d*) "Celebes form," costa and vein 1.

Larva.

Rather closely resembles that of *A. l. leucosphyrus*, its characteristic features being as follows:

(1) *Head:* *pc* rather short, not reaching the level of the bases of *ic*.

(2) *Thorax:* Prothoracic hairs 1 and 2 rather weak, hair 1 with 8–21 branches, av. 13·4 (20 specimens), and a rather fine stem; the tubercle of hair 1 with a very small apical process or none (fig. 3). Prothoracic hair 13 with fewer branches than in most other forms, only 3–6, av. 4·4 (32 specimens); rarely (3/41) with more than 5 branches and these on one side only.

(3) *Abdomen:* Palmate hairs: on seg. I, relatively undeveloped, with 6 or less branches (48/50); these often of a characteristic form, with a stiff, spine-like appearance, and with one or two markedly longer than the others; on seg. II, weakly developed, the branches

flattened or weakly lanceolate. Hair I.3 usually (35/40) simple on at least one side, very rarely (1/40) with 3 branches. Hair I.9 with 2–5 branches, usually (43/49) with no more than 3 branches on at least one side, very rarely (1/49) with 5 branches. Hair IV.13 short, half, or less than half the length of adjacent hair 12, with 3–6 branches, av. 4·8 (50 specimens); at least one side with 4 branches or more, usually (42/49) with 5 branches or more. Pecten rather variable but tends to resemble that of *A. l. leucosphyrus*.

Geographic Variation.

Geographic variation has been observed in several characters of the adult female.

(1) *Propleural hairs:* Specimens from Malaya usually (19/25) have no more than two hairs on either side, very rarely (1/25) three on both sides. Bornean specimens, however, usually (22/30) have two or more hairs on at least one side, and often (13/30) on both sides. The difference is statistically highly significant (random samples of 25 specimens of each form gave $\chi^2 = 9{\cdot}69$).

(2) *Apical wing fringe:* Specimens were seen from both areas, in which the long pale area between veins 2·2 and 3 was interrupted by dark scaling, in a manner similar to that described under *A. balabacensis*. This condition is, however, much more common in Borneo specimens—12 out of 30 specimens examined showed some degree of interruption and in five of these the pale fringe spot at vein 2.2 was completely obliterated. Of 26 Malayan specimens, examined by Mr. J. Reid (personal communication) only three were variants, and these had only a small dark patch between veins 2.2 and 3.

(3) *Maxillary index:* As shown in Table X, the number of maxillary teeth tends to be higher in specimens from Borneo; although the ranges overlap, the difference between mean values is highly significant ($t = 3{\cdot}172$).

Identification.

The adult is readily identified by the long proboscis, relatively short palps, and the degree of sub-division of the dark areas on vein 1; it bears a superficial resemblance to *A. hackeri*, but differs in the broader bands of the palps, and the presence of more than one pale interruption in MD and PAD of vein 1.

The pupa is of the "short spine IV.A" type, but on characters examined is virtually indistinguishable from that of the "Luzon form". It also closely resembles that of *A. riparis macarthuri*, but the branching of hairs II.C and V.B is diagnostic.

The larva rather closely resembles that of *A. l. leucosphyrus*, but is usually separable by the branching of abdominal hair I.9; prothoracic hair 13 is also rather characteristic, being very rarely more than five-branched. (*See* Table IV, p. 59.)

Notes.

This form was first described as a subspecies (Colless, 1948) since little was then known of its distribution. It has since been recorded from a number of countries, along with, and sometimes breeding in the same pool as, several other members of the group, including *A. l. leucosphyrus*; it is obvious then that *pujutensis* is, in fact, a good species.

A. pujutensis has in the past been not infrequently confused with *A. hackeri*—

the variant specimen of the latter mentioned by Edwards (1921) has been shown by Reid (1949) to be of the former species.

Distribution (fig. 11).

Borneo : numerous localities, in all four states. Malaya : Johore, Negri Sembilan, Selangor, Perak. Sumatra : Deli, Moeara Tebo, (Reid, 1949).

Fig. 11.—Tentative map of distribution of *A. pujutensis* (dotted line), *A. riparis macarthuri* (broken line), *A. r. riparis* and *A. cristatus* (stippled area, the latter from Mindanao only).

A. elegans James (1903).

James, S. P., *in* Theobald, F. V., 1903, *Mon. Culic.* : **3** : 51.

Type locality : India : Karwar, N. Kanara.
Types : Presumed co-type series in Brit. Mus. (Nat. Hist.) (*coll. Cogill*, 1902)

Adult female.

A large, dark, handsome species, with bold white markings, even on the mid tarsi.

Head (fig. 2): Proboscis long, 1·8–2·6, av. 2·35 mm. (18 specimens) ; dark, without any distinct pale band behind the labella, although it is faintly indicated in some specimens ; ratio proboscis/fore femur 1·16–1·30, av. 1·23 (15 specimens). Palps with normal banding, the apical pale band usually a little longer than the preapical dark ; the preapical pale band a little shorter. Palps shorter than the proboscis ; ratio palp/proboscis 0·78–0·93, av. 0·87 (15 specimens). Palp segment ratios of the *l. leucosphyrus* type (Table X). Pharyngeal teeth (1 specimen) 17 in number, 0·040 mm. long, resembling those of *balabacensis* but rather deeply dissected at apices. Maxillary index 15–16 (2 specimens).

Thorax : Integument rather darker than in most other forms. Propleural hairs 2–4, av. 2·7 (16 specimens).

Wing (fig. 10): Costa with a small PHP. Vein 1 with PSD undivided, and 1 pale interruption each in MD and PAD. ASP small, and confined to vein 1 in most specimens (14/17); subcosta and, in 8 out of 17 specimens, the costa also, with one or two small pale subsidiary interruptions in MD, distal to the ASP level. Base of *af* proximal to base of *pf*.

Legs : Hind tibia with a dark basal stripe ventrally in the apical pale band. Bands of fore and mid-tarsi well defined; hind tarsal segment IV with a prominent basal pale band, almost as long as the apical band on seg. III.

Abdomen : Scaling rather reduced dorsally; seg. VIII with only a few fine golden scales posteriorly. Ventrally, seg. VIII devoid of scales, seg. VII with a dark tuft on the posterior margin, and seg. VI with a similar, but much smaller, tuft.

Adult male.

Generally similar to the female.

Pupa (fig. 7).

One pupa, in the collection of the British Museum (Nat. Hist.) appears from its collection data to belong to this species. Its chief characteristics are:

(1) *Hair II.C :* Brush-like with about 20 branches.

(2) *Hairs III.C, IV.C, and V.B :* With 7, 4, and 5 branches respectively.

(3) *Spine IV.A :* Relatively short, ratios IV.A/III.A and IV.A/V.A are 2·0 and 0·29 respectively. Spines V.A, VI.A, and VII.A with distinct side-spicules.

(4) *Paddle teeth :* Moderately coarse; Toothed-Margin Index 0·88.

Larva.

Unknown.

Egg.

Collections from Ceylon indicate that this is the commonest, or perhaps the only member of the group occurring there. It is probable then that the description of the egg of *A.* "*leucosphyrus*" given by D'Abrera (1944) refers to *A. elegans*. If this is so, there appears to be no difference from the egg of *balabacensis*—the dimensions given by D'Abrera are as follows (8 specimens):

Length—0·53–0·56, av. 0·546 mm.

Breadth (*incl. floats*)—0·16–0·18, av. 0·173 mm.

Ratio $\frac{\textit{float length}}{\textit{egg length}}$ — av. 0·64.

Float ridges—18–19, av. 18·5.

Identification.

In the female, the long proboscis, the relatively short palps with broad pale bands, and the degree of subdivision of the dark areas of vein 1, are diagnostic. The general appearance, with bold white markings on a dark integument is also quite characteristic. The wing characters and the prominent basal band on hind tarsal seg. IV are diagnostic for the male.

The pupa is fairly well-defined by the characters described, but is not clearly separated from that of the "Fraser's Hill form" or *A. l. leucosphyrus*.

Notes.

The situation regarding the validity of the name "*A. elegans*" is exceedingly complicated, as pointed out by Reid (1949). I have been able to examine the

original specimens, and also the original correspondence between James and Theobald, and the course of events appears to have been as follows. James sent to Theobald an *MS* description and figure of a wing, plus one female specimen, suggesting that the latter might be kept as a type until further better specimens could be sent: he obviously intended to lodge a series of cotypes (James to Theobald, *in litt.* 29.xi.02). He probably had at that time at least four other female specimens (collected in October, 1902), but presumably retained them for use in preparing his forthcoming book (James and Liston, 1904). Unfortunately, the single specimen (coll. Cogill, v.02) which was sent to Theobald, and which is now in the British Museum, is of *A. l. balabacensis*, while the remainder, now also in the British Museum, are of the species described above as *A. elegans*. James' description clearly refers to more than one specimen—*vide* such words as " generally ", " sometimes ", " not constant ". His description is, moreover, at variance with his figure in several points, and the latter shows elements of both the forms concerned: on vein 1 the PAD belongs to *A. l. balabacensis*, but the PSD is undivided, as in *A. elegans*.

Theobald published the description and the figure, with the statement that " the type is in the British Museum ", but he did not label his single specimen as such, probably intending to wait for the better specimens promised by James. Unfortunately, the matter then seems to have been dropped. Subsequently, James and Liston (1904 and 1911) published descriptions which unambiguously refer to the form which I have described above, with the exception of their " variant wing ", which clearly belongs to *A. l. balabacensis*.

Under the circumstances I concur with Reid's opinion that we should consider Theobald in error in designating his single April specimen as the type, if, in fact, he can really be considered to have done so. The remaining four female and two male specimens (coll. Cogill, x.02) may then be considered as cotypes, and lectotypes chosen from them.

The status accorded to this form has varied considerably over the years. Described by James (*op.cit.*) as a species, it was treated as a synonym of *A. leucosphyrus* by James and Liston (1904), but then restored to specific status in their second edition (1911): Theobald (1910) had by then erected his new genus *Neomyzomyia*, with *elegans* as the type species. Subsequently, it was once more synonymised with *A. leucosphyrus* by James and Stanton (1912), until Reid (1949) discovered new criteria for treating it as a distinct " variety ", and revived the name.

Subsequent investigations show that *elegans* possesses quite distinctive taxonomic features and is sympatric with *l. balabacensis*; it is therefore treated as a good species in this paper. It appears to be the dominant, or the only, member of the group present in Ceylon and it seems likely that it originated in that island, later spreading to the S.W. coast of India.

It should be noted that its re-instatement makes it once more the type species of the group *Neomyzomyia*, although, as pointed out by Christophers (1933), the validity of the group name itself is highly questionable.

Distribution (fig. 12).

India: Karwar, Travancore. Ceylon: numerous localities.

A. hackeri Edwards (1921).

Edwards, F. W., 1921, *Bull. ent. Res.* **12** : 70. (*A. leucosphyrus* var. *hackeri*.)

Type locality : Federated Malay States.
Types : Female in British Museum (Nat. Hist.).

Adult female.

Head (fig. 2) *:* Proboscis long, 2·3–2·6, av. 2·45 mm. (15 specimens), with a narrow ring of golden scales apically, behind the labella. Palps relatively short, with very narrow pale bands, the apical segment merely tipped with white ; seg. 5 relatively short (*see* Table X). Ratios : Palp/proboscis 0·67–0·78, av. 0·73 ; proboscis/fore femur 1·27–1·40, av. 1·28 (15 specimens). Pharyngeal teeth of much the same shape as in *l. balabacensis*, 16–19 in number, av. 17·2, length 0·04–0·05, av. 0·044 mm. (6 specimens). Maxillary index 13–18, av. 15·2 (12 specimens).

Thorax : Integument generally dark. Propleural hairs 3 or 4, rarely (1/15) 2 : 2.

Wing (fig. 10) : Length 3·2–3·8, av. 3·44 mm. (10 specimens). Costa usually (9/10) with a small PHP on at least one wing. ASP small, usually much shorter than the basal stub of MD and sometimes reduced to only 1 or 2 pale scales ; usually (11/15) confined to vein 1, rarely (1/15) reaching costa on one wing only. Costa and/or subcosta of at least one wing occasionally (6/19) with a very small additional pale spot in MD, distal to the ASP level (cf. *A. elegans*). Vein 1 with PSD undivided, MD and PAD each with one pale interruption. Base of *af* distinctly proximal to base of *pf*.

Legs : Speckling rather reduced. Apical pale band of hind tibia with dark longitudinal stripe on the ventral aspect. Hind tarsal seg. IV with a basal pale band, this sometimes reduced to a minute patch.

Abdomen : Dorsally, scaling rather reduced ; seg. VIII with only a few pale scales posteriorly. Ventrally, seg. VII with only a sparse tuft of dark scales or none.

Adult male.

Generally similar to female, but most specimens (possibly all, if fresh) show an ill-defined stripe of pale scaling dorsally on the basal one third to two-thirds of the proboscis. ASP rather prominent, frequently (10/15) involving the costa of at least one wing. PAD of costa sometimes (6/15) interrupted by a small pale spot on one or both wings. Hind tarsal seg. IV usually (14/25) without a basal pale band on either leg.

The terminalia show no differences from *l. balabacensis*.

Pupa (fig. 7).

Characteristic features are :

(1) *Hair II.C:* With some 15–25 branches, arranged more or less in one plane along 1 or 2 main stems.

(2) *Hairs III.C and IV.C :* With 7–23, and 4–16 branches respectively. (*See* Geographic Variation.)

(3) *Spine IV.A :* Very short. Ratios : IV.A/III.A 1·00–1·75, av. 1·30 ; IV.A/V.A 0·09–0·18, av. 0·14 (13 specimens).

(4) *Paddle teeth :* Rather fine ; T.M. index 0·77–0·83, av. 0·79 (13 specimens).

Larva.

Very dark, often with conspicuous pale spots or bands on the dorsal surface.

Head : *ic* and *oc* simple ; *pc* long, reaching well past the anterior margin of the head, usually simple but sometimes (7/20) with 2 or 3 apical branches on one or both sides (fig. 4).

Thorax : Prothoracic hair 1 with broad flattened stem and 17–25 branches, av. 20·9 (20 specimens) ; basal tubercle with a distinct apical tooth, but this much less prominent

than in *A. l. balabacensis* (fig 3). Metathoracic palmate hair weakly developed with 6–12 long, attenuated, lanceolate branches, av. 8·8 (13 specimens).

Abdomen : Abdominal palmate hair on seg. I more or less undeveloped ; on seg. II, rather smaller than on following segments, but fully developed with clearly differentiated filaments (fig. 4). Hair IV.13 simple or bifid, av. 1·8 branches (13 specimens) ; very strongly developed and longer than adjacent hair 12. Pecten teeth long, subequal.

Egg.

Mr. J. Reid has kindly made available a series of eggs laid by 4 females taken at Rantau Panjang, Selangor. These show no difference in ornamentation, etc., from the egg of *A. l. balabacensis*, but are distinctly longer and relatively narrower. Measurements are given in Table VI below, of 12 eggs, taken at random from the 4 batches ; the corresponding dimensions for *A. l. balabacensis* are also shown for comparison.

TABLE VI.—*Dimensions of eggs of* A. hackeri *and* A. l. balabacensis.

	A. hackeri.		*A. l. balabacensis.*	
Dimension.	Range.	Mean.	Range.	Mean
Length . .	0·60–0·65 mm.	0·613 mm.	0·49–0·57 mm.	0·526 mm.
Breadth (including floats)	0·19–0·20 mm.	0·196 mm.	0·18–0·21 mm.	0·194 mm.
Float length . .	0·38–0·46 mm.	0·414 mm.	0·28–0·36 mm.	0·318 mm.
Float ridges . .	18–20	18·5	14–19	16·4

Geographic Variation.

Adults from Malaya and Borneo differ to some extent in the number of pharyngeal teeth and a marked difference is found in the pupae in the branching of hairs III.C and IV.C. The relevant figures are shown in Table VII below.

TABLE VII.—*Geographic variation in* A. hackeri *pupae.*

	Borneo.		Malaya.	
Character.	Range.	Mean.	Range.	Mean.
Pupal hair III.C . .	14–23	16·6 (10)	7–12	9·3 (3)
,, hair IV.C . .	6–16	9·9 (10)	4– 8	6·5 (3)
Adult, pharyngeal teeth	16–19	17·1 (7)	13–16	15·0 (5)

(Number of specimens shown in brackets.)

Though based on small numbers of specimens, the differences seem significant (" t " for pharyngeal teeth means = 2·80) and are apparently instances of the normal process of divergence in geographically isolated forms.

Identification.

The relatively long proboscis and short palps with very narrow bands distinguish the female of *hackeri* from most other forms ; other characteristic features are the apical pale ring on the proboscis, and vein 1 with only one pale interruption each in MD and PAD, and none in PSD. The latter differentiates *hackeri* from the very similar " Celebes form ". The male is identifiable by the ornamentation of wing and proboscis; separation from *A. elegans* is difficult,

but the more prominent basal pale band on hind tarsal seg. IV of the latter is fairly characteristic.

Pupae of the Borneo form are readily identified by the strong branching of hair III. C, but Malayan specimens rather closely resemble *A. riparis macarthuri*; the latter has rather fewer branches to hairs III. C and IV. C but the difference is statistical only.

In the larva, the length, branching, and position of the post-clypeal hairs, and the well-developed abdominal palmate II, are diagnostic; also in living specimens, the colour pattern. Occasional specimens of *l. balabacensis* may bear

FIG. 12.—Tentative map of distribution of (1) *A. elegans*; (2) *A. hackeri**; (3) the "Celebes form."
* See footnote on p. 81.

a superficial resemblance to *hackeri*, but examination of prothoracic hair 1 and abdominal hair IV. 13 will give a complete separation in such cases.

Notes.

A. hackeri was originally described as a "variety" of *A. leucosphyrus*, but this was partly due to the inclusion of a specimen of *A. pujutensis* in the type series. It is obvious, however, that it is a good species by all modern criteria and the varietal designation should now be dropped.

Although usually considered a rare species, areas of local abundance are known on the coast of Malaya (Institute for Medical Research, 1951). More thorough search, particularly in Nipah palm areas, may reveal that this species is, in fact, quite common.

Distribution (fig. 12).[7]

Borneo : North Borneo (Tambunan), Sarawak (Lg. Tebangan), Pulau Laut. Malaya : numerous localities. Probably also Sumatra (Swellengrebel and Rodenwaldt, 1932 ; Bonne-Wepster and Swellengrebel, 1953).

" *A. leucosphyrus*, Celebes form "

" *A. leucosphyrus var. hackeri* " from Celebes, auct.

Only one specimen, a female, has been seen ; Mr. J. Reid has kindly supplied further information concerning three female specimens in the Institute for Tropical Hygiene, Amsterdam.

This form closely resembles *A. hackeri*, its chief characteristics being as follows :

Adult female.

Head : Palps and proboscis identical with *hackeri*. Ratios : palp/proboscis 0·78, proboscis/fore femur 1·26 (1 specimen). Palp segment ratios : *3/5*, 3·1 ; *3/4*, 1·7 (1 specimen).

Wing (fig. 10) : Resembles that of *l. balabacensis*, with a general tendency towards subdivision of the dark areas. Vein 1 with 1–3 pale interruptions in PSD, 2–4 in MD, and 3–6 in PAD ; PSD longer basally than the corresponding costal spot. ASP confined to vein 1 ; an additional small pale spot present in the basal stub of MD (1 specimen).

Leg : Hind tibia with the broad apical pale band interrupted ventrally, much as in *A. hackeri* ; however, instead of the linear extension of the dark scaling found in the latter there is a discrete oval patch of dark scales in the white (4/4) (fig. 9). Hind tarsal seg. IV without a basal pale band (1/1).

Abdomen : Dorsally, seg. VIII with a fair covering of narrow golden scales on the posterior half. Ventrally, seg. VII with a rather prominent tuft of dark scales.

Identification.

The female is readily identified by its long proboscis, and palps with very narrow pale bands, as in *A. hackeri* ; also the presence of one or more pale interruptions in the PSD of vein 1, and more than one in MD and PAD of the same vein. The male probably shows these characters also. Larval and pupal characters are not known.

Notes.

The possibility of this form being a distinct species or subspecies was suggested by Colless (1948) on purely theoretical grounds ; at the same time, Reid (1949) independently produced evidence that this was, in fact, the case.

Judging from its distinct morphological characteristics, it is almost certainly a good species—its nearest relative would appear to be *A. hackeri*, but it is so clearly distinct from this species, both in morphology and biology, that there appear to be no grounds for awarding it less than specific rank. Its formal recognition as such must, however, be postponed until more specimens are available, and its characteristics more accurately evaluated.

The form appears to be confined to Celebes and some neighbouring islands.

[7] I have since seen one female of this species, with correlated larval skin, in the British Museum, collected from Irahnan R., Palawan, S. Philippines.

Swellengrebel and Rodenwaldt (1932), in their records of *A.* "*leucosphyrus*" from Celebes, show all but one as "*var. hackeri*", and Overbeek (1941) records dissections of this variety. It may be presumed that most, if not all, of these refer to the form described above.

Distribution (fig. 12).

Celebes: Aalo, Kaboena, Boeton; Lindoe Meer. Probably also Sanghir and Talaud Is. (Swellengrebel and Rodenwaldt, 1932).

A. "*leucosphyrus*", larval form from Palembang.

A number of preserved larvae, collected at Palembang, Sumatra (19.iii.27), have been found in the collection of the Department of Parasitology, University of Malaya. These appear closest to *A. l. leucosphyrus*, as described above, but differ somewhat in several important characters. Their main features are as follows (10 specimens):

Head: *pc* as in *l. leucosphyrus*.

Thorax: Prothoracic hair 1 resembling that of *l. leucosphyrus* but the apical tooth of the basal tubercle variable, resembling *l. balabacensis* in 1 out of 10 specimens, *l. leucosphyrus* in 1 out of 10, the remainder with a weak but quite distinct tooth.

Abdomen: Hair IV.13 with 3–6 branches, av. 4·6, 4 or more on at least one side, the hair about half as long as adjacent hair 12. Hair I.9 3–5-branched, av. 3·3. Abdominal palmate hair on seg. II with weakly lanceolate leaflets.

This may be the larva of the Sumatran *l. leucosphyrus*, differing from the Malayan form by a somewhat stronger development of the basal tubercle of prothoracic hair 1; there are unfortunately no correlated adults. Also it is not impossible that they are the larvae of an aberrant form of *l. balabacensis* or some other species.

6. Intra-Group Relationships.

No systematic study of a group of related forms can be considered complete without some analysis of internal relationships and phylogeny; hence no apology is needed for the following section, despite its generally speculative nature.

One of the most obvious facts emerging from taxonomic studies in this group is the general lack of correlation between morphological characters in the various forms: that is to say, subdivision of the group according to one character, *e.g.* the nature of PSD, vein 1, differs from the grouping obtained using another, *e.g.* relative length of proboscis. This applies to both adult and immature stages. Generally, the taxonomically useful characters appear to be entirely trivial in the sense that they show no obvious adaptational significance, and appear to have arisen in a somewhat random fashion at various levels in the evolutionary history of the group. There is, moreover, little indication of correlation between morphology and biology or distribution, with the one exception mentioned below.

While these taxonomically useful characters appear to be mainly non-adaptive, it is not unreasonable to assume that they are external expressions of balanced gene-complexes which *are* adapted to particular environments. Thus

the seemingly random development of such characters suggests that a significantly large random element occurs in the gene-complex as a whole; this in turn suggests that evolutionary "drift" (the Sewall-Wright effect) has played a large part in the evolution of the group.

The exception mentioned above is the general tendency of Philippine forms to have the proboscis short as compared with the fore femur. This is illustrated in figure 13, which shows the various forms arranged in order of decreasing proboscis/fore femur ratios. There appear to be three groups: (a) *A. pujutensis*, *A. hackeri*, the "Celebes form", and *A. elegans*; (b) the *A. leucosphyrus* subspecies, with the exception of the "Negros" and "Luzon" forms; (c) these two latter forms (the "Luzon form" is rather intermediate), the *A. riparis* subspecies, and *A. cristatus*. It is immediately noticeable that all four

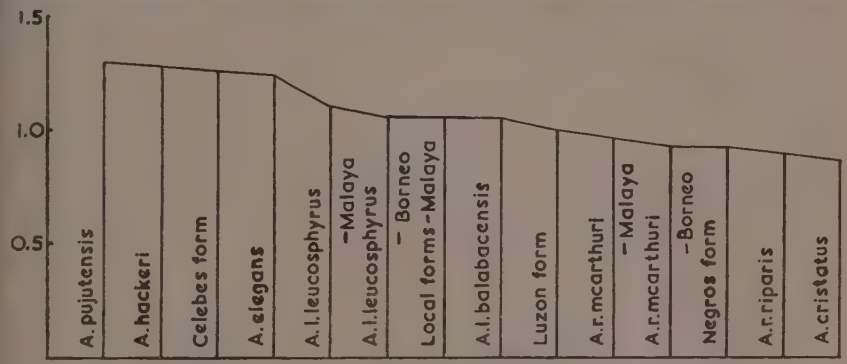

FIG. 13.—Forms of *A.* "*leucosphyrus*" arranged in decreasing order of proboscis/fore femur ratio.

forms from the Philippines proper fall in group (c)—*A. l. balabacensis* does extend to Palawan, but this island is zoogeographically a part of Borneo. Also, in the three geographic forms of *A. riparis* there is a clinal decrease in this ratio from Malaya towards the Philippines. This evidence suggests that relative proboscis length has a significant survival value, direct or indirect, and that the Philippine forms have undergone convergent adaptation to conditions peculiar to that area. The factors conditioning such adaptation, however, remain completely obscure.

The above grouping, by relative length of proboscis, is further illustrated in figure 14, in which mean proboscis length of each form is plotted against mean lengths of fore femur on a logarithmic scale. Logarithms have been used since analysis of a number of series shows that the relationship between these measurements is allometric—regression coefficients of log. proboscis on log. femur were as follows:—

A. l. balabacensis, Borneo (15 specimens)	0·95
A. pujutensis (15 specimens)	0·78
A. r. macarthuri Borneo (17 specimens)	0·65
A. l. leucosphyrus Borneo (16 specimens)	0·63
A. hackeri (15 specimens)	0·63

Figure 14 shows much the same grouping as before, but the " Luzon form " is more clearly related to the other subspecies of *A. leucosphyrus*. The two upper groups are quite clear-cut, with the forms within each group showing a constant relationship ; the third group, while less well-defined, tends to follow the same pattern. In each group the regression coefficient approximates to unity, which is rather higher than those quoted above but due, in part at least, to the use of arithmetic means instead of geometric. Thus the groups resolve into three levels of relative proboscis length with differences within the groups conditioned largely by *absolute* size.

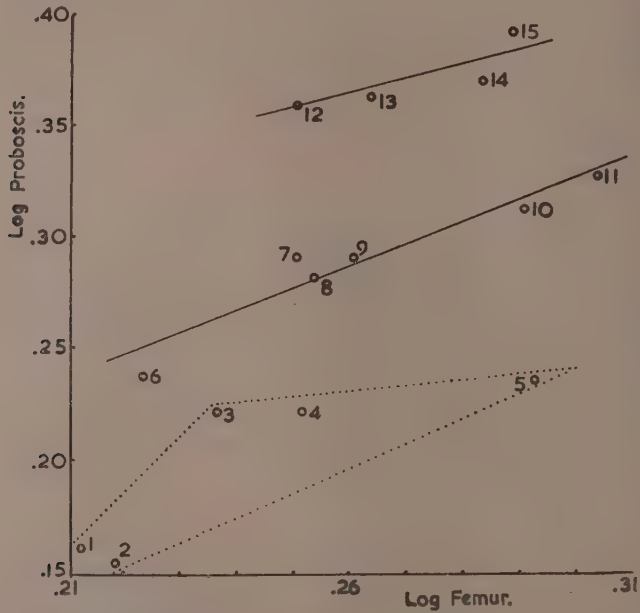

Fig. 14.—Average lengths of proboscis and fore femur, plotted on a logarithmic scale: 1 = *A. riparis riparis* ; 2 = *A. cristatus* ; 3 = *A. r. macarthuri* (Malaya) ; 4 = the " Negros form " ; 5 = *A. r. macarthuri* (Borneo) ; 6 = the " Luzon form " ; 7 = *A. leucosphyrus leucosphyrus* (Malaya) ; 8 = *A. l. balabacensis* ; 9 = the " Fraser's Hill form " ; 10 = *A. l. leucosphyrus* (Borneo) ; 11 = the " Kepong form " ; 12 = *A. pujutensis* ; 13 = the " Celebes form " ; 14 = *A. elegans* ; 15 = *A. hackeri*. The sloping lines show regression of the log proboscis on log femur ; the dotted lines merely enclose the lower group.

One feels that the above grouping (of figure 14) is of a more fundamental nature than any other tested, particularly since it includes the obviously close relationship between the adults of *A. hackeri* and the " Celebes form " ; the various forms of *A. leucosphyrus* ; and the *A. riparis* subspecies and *A. cristatus*. The position of the " Negros form " is anomalous, but it has been plotted from a single poor specimen and may be inaccurate ; on the basis of general resemblance in other characters it must be considered a form of *A. leucosphyrus*.

Using this grouping, a tentative phylogenetic scheme may be derived, using no mechanism of speciation other than that by geographic isolation, with subsequent divergence due to altered selection pressures and random " drift ". The geological history and present geography of the Malayan sub-region have afforded ample scope for the development of endemic forms in isolated areas with subsequent mixing by immigration or breakdown of natural barriers. Such barriers have not necessarily been formed by the sea, since the jungle-breeding habit, common to all forms, could produce isolation within climatic zones.

The history of the group appears to commence with the division of an ancestral stock into three main lines—the *hackeri*, *riparis*, and *leucosphyrus* stocks. The latter stock is probably the oldest—it now has the widest distribution of the three (fig. 8), and, moreover, the other two lines show distinct morphological resemblances and a tendency to geographic separation. If this is so it is at first sight surprising that so little definite speciation has occurred within *A. leucosphyrus*. But if we may judge from present conditions this line may always have been the most vigorous and " biologically successful ", thereby maintaining larger and more widespread populations. A tendency to form subspecies rather than species would then be a logical consequence of large population-size and widespread distribution, whereby migration pressure reduces the effectiveness of isolation, especially when isolating barriers are formed by relatively narrow arms of the sea. Large populations are also less subject to random " drift ".

A. l. balabacensis appears to be the oldest, if not the parent form, of the *leucosphyrus* line. It has the widest distribution in the whole group and, although its range is now broken by that of *A. l. leucosphyrus*, there has been only slight divergence in the parts thus isolated. The Philippine forms probably developed *in situ* from a *balabacensis*-like parent, while *l. leucosphyrus* arose during isolation somewhere in the vicinity of Sumatra. The latter form re-colonised the Malay Peninsula where, presumably on account of superior adaptation to local conditions, it became established in the south. It had, however, not achieved complete genetic isolation from *l. balabacensis* and a zone of secondary intergradation arose in the northern half of Malaya proper.

In Borneo, however, it appears that *l. leucosphyrus* arrived in a form genetically isolated from the local *l. balabacensis*. Possibly, it reached that country later than Malaya, in accordance with the present relative distances from Sumatra. There was no interbreeding of the two forms and *l. balabacensis* was replaced, over most of Sarawak at least, until a barrier was reached in the north of that state. The conditions limiting *l. leucosphyrus* to its present range are obscure—the only common factor to be seen in the areas concerned (and not shared by others) is that they coincide roughly with the drainage system of the ancient river which flowed north through what is now the China Sea.

In the *hackeri* line, *A. elegans* appears to have been differentiated at an early stage during isolation in Ceylon and/or the S.W. coast of India. The other branch produced *A. hackeri*, which was forced, presumably by competition, into a restricted ecological niche as a bamboo and palm axil-breeder ; some other members of the group are facultative breeders in such sites. The " Celebes form " probably developed from *hackeri* at a relatively recent date after colonisation across Wallace's line, and is the only member of the group known to have

achieved the crossing. Brug and Bonne-Wepster (1947) record the interesting possibility of mosquito migration between Borneo and Celebes on the " floating islands " of Nipah palm which are commonly seen in Macassar Straits. As *hackeri* is known to breed in the bases of these palms, it seems possible that the *hackeri*-like colonists of Celebes came from Borneo, and in such a fashion.

The case of *A. pujutensis* is more difficult. Its inclusion in the *hackeri* line is based on little more than relative proboscis length, a resemblance which may be the result of convergence rather than close-relationship ; the " Negros form " shows a similar anomaly in the opposite direction. Its present distribution (fig. 11), which coincides almost exactly with that of *hackeri* (fig. 12), makes any recent derivation from that line unlikely. Possibly it represents an early stage in the development of the *hackeri* stock, restrained from further speciation by the conditions mentioned above for *A. l. leucosphyrus*.

In the *riparis* line, *A. cristatus* appears to be an endemic development from an early *riparis*-like colonist of Mindanao. Its very distinctive larval characters are presumably the result of " drift " in a rare species—*A. stookesi*, a recently described *Neomyzomyia* from Borneo, shows a close analogy in its differences from the related *A. watsoni*. Within *A. riparis* the two subspecies (one with two geographic forms) are an obvious example of geographic differentiation, with some clinal features. Its wide range, with what appear to be distinct gaps, suggests an " old " species, now suffering competition from forms better adapted to parts of its original range.

The above outline, though highly speculative, does help to ally these mosquitoes with the large group of animal forms in which speciation is believed to have occurred during geographic isolation. It is obvious, however, that definite conclusions must await, firstly, more detailed knowledge of the morphology, biology and distribution of the group, and secondly, some form of genetic analysis of its members.

7. Summary.

(1) Descriptions are given of the various members of the *A. leucosphyrus* group of Oriental Anophelines, together with systematic notes and keys for the identification of females and larvae. The following forms are treated :

A. leucosphyrus leucosphyrus Dönitz, 1901.
A. l. balabacensis Baisas, 1936.
A. leucosphyrus " Luzon form ".
" " Negros form ".
" " Fraser's Hill form ".
" " Kepong form ".
A. riparis riparis King and Baisas, 1936.
A. riparis macarthuri subsp. n.
A. cristatus King and Baisas, 1936.
A. pujutensis, Colless, 1948.
A. elegans, James, 1903.
A. hackeri Edwards, 1921.
A. " *leucosphyrus* " " Celebes form ".

(2) The occurrence of geographic variation is demonstrated in a number of forms.

(3) The proboscis/fore femur ratio, an important taxonomic character, is shown to vary allometrically and is used for subdivision of the group. A low value of this ratio appears to have positive survival value in the Philippines.

(4) A tentative scheme of internal relationships and evolutionary history is described, with geographic isolation as the major factor producing differentiation of new forms.

TABLE VIII.—*Adult dimensions.*

Form.	Number examined.	Length in mm. Wing.	Proboscis.	Palp.	Fore femur.
A. l. balabacensis	66	3·1–4·0, *3·44*	1·5–2·4, *1·92*	1·4–2·4, *1·83*	1·5–2·4, *1·79*
A. l. leucosphyrus :					
Malaya	15	2·7–3·4, *3·08*	1·7–2·1, *1·96*	1·4–2·0, *1·72*	1·5–2·1, *1·78*
Borneo	16	3·2–4·0, *3·62*	1·8–2·2, *2·06*	1·7–2·0, *1·86*	1·8–2·2, *1·95*
A. leucosphyrus :					
" Luzon form "	5	2·8–3·3, *3·07*	1·6–2·0, *1·73*	1·2–1·9, *1·52*	1·3–2·0, *1·67*
" Negros form "	1	.	1.7	1·7	1·8
" Fraser's Hill form "	7	3·4–3·6, *3·46*	1·9–2·1, *1·96*	1·5–2·1, *1·81*	1·5–2·1, *1·82*
" Kepong form "	6	3·4–3·6, *3·54*	2·0–2·3, *2·13*	1·9–2·2, *2·01*	1·9–2·2, *2·01*
A. riparis riparis	3	. 3·0*	1·4–1·5, *1·45*	1·4–1·5, *1·41*	1·5–1·8, *1·63*
A. r. macarthuri :					
Malaya	9	3·0–3·5, *3·29*	1·5–1·8, *1·67*	1·4–1·8, *1·57*	1·5–1·9, *1·72*
Borneo	18	3·2–4·0, *3·62*	1·6–2·0, *1·72*	1·5–1·9, *1·70*	1·6–2·2, *1·96*
A. cristatus	5	. 3·1*	1·3–1·5, *1·43*	1·2–1·5, *1·34*	1·5–1·7, *1·65*
A. pujutensis	15	3·0–3·5, *3·33*	1·9–2·5, *2·29*	1·6–2·1, *1·88*	1·5–2·0, *1·78*
A. elegans	18	2·9–3·8, *3·37*	1·8–2·6, *2·35*	1·5–2·3, *2·02*	1·6–2·2, *1·92*
A. hackeri	15	3·2–3·8, *3·44*	2·3–2·6, *2·47*	1·6–2·0, *1·80*	1·8–2·0, *1·94*
A. " leucosphyrus " :					
" Celebes form "	1	3·2	2·3	1·8	1·8

* From 1 specimen only. Means are in italic figures.

TABLE IX.—*Palp/proboscis/fore femur ratios.*

Form.	Number of specimens.	Palp/proboscis. Range.	Mean.	Stand. devn.	Proboscis/fore femur. Range.	Mean.	Stand. devn.
A. l. balabacensis :							
Assam	13	0·92–1·00	*0·95*	*0·034*	1·02–1·10	*1·06*	*0·031*
Burma	13	0·85–0·98	*0·93*	*0·050*	1·01–1·14	*1·07*	*0·038*
N.Malaya	10	0·91–1·00	*0·96*	*0·031*	1·00–1·10	*1·07*	*0·030*
Java	8	0·83–0·94	*0·89*	*0·035*	0·99–1·13	*1·07*	*0·045*
Borneo	15	0·90–1·00	*0·95*	*0·028*	1·02–1·09	*1·06*	*0·027*
Balabac	3	0·95–0·96	*0·95*	*0·007*	1·02–1·06	*1·04*	*0·021*
Overall	62	0·83–1·00	.	.	0·99–1·14	.	.
A. l. leucosphyrus :							
Borneo	15	0·86–0·99	*0·91*	*0·033*	1·00–1·11	*1·05*	*0·037*
Malaya	15	0·80–0·96	*0·88*	*0·039*	1·06–1·14	*1·10*	*0·032*
Overall	30	0·80–0·99	.	.	1·00–1·14	.	.
A. leucosphyrus :							
"Luzon form"	4	0·84–0·95	*0·91*	*0·054*	0·96–1·05	*1·00*	*0·037*
"Negros form"	1	.	*1·00*	.	.	*0·93*	.
"Fraser's Hill form"	8	0·84–1·00	*0·92*	.	1·02–1·15	*1·09*	.
"Kepong form"	6	0·91–0·96	*0·94*	.	1·03–1·09	*1·06*	.
A. riparis riparis	3	0·94–1·00	*0·97*	*0·030*	0·87–0·92	*0·89*	*0·025*
A. riparis macarthuri :							
Borneo	18	0·88–0·98	*0·93*	*0·034*	0·88–1·00	*0·93*	*0·036*
Malaya	9	0·87–0·98	*0·94*	*0·052*	0·91–1·03	*0·97*	*0·038*
Overall	27	0·87–0·98	.	.	0·88–1·03	.	.
A. cristatus	5	0·90–1·00	*0·94*	*0·041*	0·85–0·90	*0·87*	*0·022*
A. pujutensis	15	0·72–0·87	*0·83*	*0·035*	1·24–1·38	*1·29*	*0·046*
A. elegans	15	0·84–0·93	*0·87*	*0·029*	1·16–1·30	*1·23*	*0·040*
A. hackeri	15	0·67–0·78	*0·73*	*0·036*	1·21–1·40	*1·28*	*0·058*
A. "leucosphyrus" :							
"Celebes form"	1	.	*0·78*	.	.	*1·26*	.

TABLE X.—*Palp segment ratios, pharyngeal teeth, and maxillary indices.*

Form.	Number of specimens.	Palp segment ratios. 3/5.	Palp segment ratios. 3/4.	Pharyngeal teeth. Number.	Pharyngeal teeth. Length (mm.)	Maxillary Index.
A. l. balabacensis :						
Mainland	10	2·2–2·5, *2·31*	1·5–1·7, *1·55*	13–15, *14·0*	0·03–0·05, *0·042*	11–16, *13·3*
Borneo	10	2·4–2·9, *2·65*	1·6–1·9, *1·73*	12–15, *13·7*	0·04–0·06, *0·044*	11–15 *13·2*
Java	3	2·7–3·3, *2·93*	1·7–1·9, *1·80*	. *12·0*	0·03–0·04, 0·*039*	13–15, *14·0*
Overall	23	2·2–3·3, .	1·5–1·9, .	12–15, .	0·03–0·06, .	11–16, *13·8*
A. l. leucosphyrus :						
Malaya	5	2·5–2·8, *2·70*	1·6–1·8, *1·69*	14–16, *15·1*	0·05–0·06, *0·052*	15–18, *16·9*
Borneo	5	2·4–2·7, *2·52*	1·6–1·8, *1·70*	14–16, *14·8*	0·05–0·06, *0·053*	15–18, *16·8*
Overall	10	2·4–2·8, *2·61*	1·6–1·8, *1·70*	14–16, *14·9*	0·05–0·06, *0·053*	15–18, *16·9*
A. leucosphyrus :						
"Luzon form"	1	2·50	1·60	10·0	0·034	18·0
"Fraser's Hill form"	6	2·5–2·9, *2·70*	1·6–1·7, *1·68*	16–20, *17·3*	0·04–0·06 *0·051*	16–18 *17·2*
"Kepong form"	4	2·3–2·4, *2·37*	1·4–1·6, *1·53*	12–18, *15·3*	0·04–0·05, 0·*049*	16–18, *16·7*
A. riparis riparis	1	3·1	1·9	.	.	20·5
A. riparis macarthuri :						
Malaya	5	3·0–3·6, *3·17*	1·8–2·1, *1·72*	11–13, *12·0*	0·03–0·04, *0·038*	21–24, *22·1*
Borneo	5	3·0–3·3, *3·14*	1·7–1·9, *1·82*	10–12, *11·4*	0·03–0·04, *0·036*	21–28 *24·0*
Overall	10	3·0–3·6, *3·16*	1·7–2·1, *1·77*	10–13, *11·7*	0·03–0·04, *0·037*	21–28, *23·1*
A. cristatus	1	3·3	2·2	.	.	21·5
A. pujutensis :						
Malaya	8	2·4–3·0, *2·69*	1·4–1·7, *1·63*	16–20, *18·5*	0·04–0·05, *0·047*	14–19, *16·4*
Borneo	12	2·3–2·9, *2·60*	1·5–1·7, *1·60*	15–19, *17·7*	0·05–0·06, *0·054*	14–16, *14·5*
Overall	20	2·3–3·0, *2·64*	1·4–1·7, *1·61*	15–20, *18·0*	0·04–0·06, *0·051*	14–19, *15·3*
A. elegans	2	2·4–2·7, *2·55*	1·6–1·7, *1·65*	. 17·0*	. 0·040*	15–16, *15·5*
A. hackeri :						
Malaya	5	2·7–3·9, *3·15*	1·7–2·2, *1·79*	13–16, *15·0*	0·04–0·05, *0·040*	13–18, *15·3*
Borneo	7	2·6–3·6, *3·26*	1·8–2·0, *1·86*	16–19, *17·1*	0·04–0·05, *0·043*	13–18, *15·1*
Overall	12	2·6–3·9, *3·21*	1·7–2·2, *1·83*	13–19, .	0·04–0·05, *0·042*	13–18, *15·2*
A. "leucosphyrus" :						
"Celebes form"	1	3·1	1·8	1·7	.	.

Means are in italic figures.
Counts and measurements made on dissected parts, mounted in balsam.
*Single specimen.

TABLE XI.—*Larval dimensions.*

Form.	Number of specimens.	Antennae length (mm.).	Hair IV.12 length (mm.).	Hair IV.13 length (mm.).	IV.13 / IV.12
A. l. balabacensis	20	0·25–0·32, *0·289* (57)	0·24–0·33, *0·28*	0·16–0·29, *0·19*	0·5–0·9, *0·69*
A. l. leucosphyrus :					
Malaya	10	0·24–0·30, *0·278*	0·20–0·25, *0·23*	0·07–0·13, *0·11*	0·3–0·7, *0·48*
Borneo	13	0·25–0·28, *0·265*	0·19–0·28, *0·23*	0·09–0·16, *0·12*	0·4–0·7, *0·55*
A. leucosphyrus :					
"Luzon form"	6	0·27–0·32, *0·288* (9)	0·27–0·35, *0·30*	0·12–0·18, *0·17*	0·3–0·7, *0·57*
"Negros form"	3	0·30–0·31, *0.307*	0·30–0·32, *0·31*	0·18–0·25, *0·21*	0·6–0·8, *0·67*
"Fraser's Hill form"	5	0·32–0·35, *0·331* (10)	0·28–0·33 *0·31*	0·24–0·33, *0·29*	0·8–1·2, *0·94*
"Kepong form"	6	0·28–0·31, *0·298*	0·22–0·27, *0·24*	0·10–0·13, *0·12*	0·4–0·6, *0·50*
A. riparis riparis	5	0·24–0·27, *0·260* (9)	0·23–0·30, *0·27*	0·13–0·22, *0·18*	0·5–0·9, *0·68*
A. riparis macarthuri :					
Malaya	10	0·23–0·29 *0·263* (20)	0·20–0·28, *0·23*	0·06–0·12, *0·08*	0·2–0·4, *0·35*
Borneo	10	0·24–0·27, *0·256*	0·19–0·26, *0·24*	0·08–0·14, *0·12*	0·4–0·6, *0·49*
A. cristatus	5	0·23–0·26, *0·245* (10)	0·17–0·27, *0·21*	0·23–0·33, *0·28*	1·1–1·7, *1·36*
A. pujutensis	10	0·24–0·31, *0·277* (20)	0·22–0·31, *0·26*	0·08–0·13, *0·10*	0·3–0·5, *0·40*
A. hackeri	5	0·27–0·33, *0·279* (13)	0·23–0·27, *0·25*	0·32–0·33, *0·33*	1·3–1·4, *1·32*

Means are in italic figures ; number of specimens as given, unless otherwise shown in brackets.

TABLE XII*a*.—*Larval chaetotaxy.*

Hair.		*A. l. leucosphyrus*, Malaya.	*A. l. leucosphyrus*, Borneo.	*A. leucosphyrus*, "Luzon form."	*A. leucosphyrus*, "Fraser's Hill form."	*A. leucosphyrus* "Kepong form."
Prothor.	1	11–17, *13·7*	11–17, *14·1*	14–20, *16·6*	15–23, *18·8*	11–21, *13·9*
,,	2	8–12, *10·7*	6–13, *9·8*	11–16, *13·9*	8–14, *10·7*	8–12, *9·2*
,,	13	4–7, *6·1*	4–7, *6·2*	5–7, *5·8*	6–10, *8·3*	6–10, *7·6*
Metathor.	1	5–12, *8·0*	5–11, *7·7*	4–8, *5·5*	2–5, *3·4*	3–5, *3·8*
Abdom.	I. 3	1–4, *1·3*	1–3, *1·5*	1–2, *1·2*	1–1, *1·0*	2–4, *2·9*
,,	I. 9	3–7, *4·8*	4–7, *5·4*	3–5, *3·6*	3–6, *4·6*	5–6, *5·1*
,,	II.13	4–6, *4·9*	4–9, *5·4*	4–7, *4·9*	3–5, *3·5*	3–5, *3·7*
,,	III. 6	11–18, *13·9*	13–20, *16·1*	12–18, *14·8*	14–20, *16·0*	16–20, *18·6*
,,	III. 9	6–11, *8·2*	7–12, *9·1*	4–8, *6·4*	7–10, *7·5*	6–11, *8·9*
,,	IV. 6	2–3, *2·3*	2–3, *2·3*	2–3, *2·1*	2–3, *2·1*	2–3, *2·3*
,,	IV. 9	5–11, *8·4*	7–12, *9·0*	5–9, *6·8*	6–9, *6·6*	8–10, *9·2*
,,	IV.13	2–6, *4·2*	2–5, *3·9*	3–5, *3·3*	3–4, *3·1*	3–4, *3·8*
,,	V. 6	1–3, *2·0*	2–3, *2·4*	1–3, *1·9*	2–3, *2·1*	2–3, *2·2*
Number of specimens		12	13	9	10	6

Means are in italic figures.

TABLE XII*b*.—*Larval chaetotaxy.*

Hair.		*A. riparis riparis.*	*A. r. macarthuri*, Malaya.	*A. r. macarthuri*, Borneo.	*A. cristatus.*	*A. pujutensis.*	*A. hackeri.*
Prothor.	1	11–21, *15·3*	12–21, *16·7*	13–18, *15·4*	14–20, *16·5*	8–21, *13·4* (20)	17–25, *20·9* (20)
,,	2	8–14, *11·2*	9–14, *12·1*	8–14, *11·1*	10–17, *12·6*	9–15, *10·8* (20)	13–17, *14·9*
,,	13	4–6, *4·8*	4–7, *5·2*	4–6, *4·6*	6–10, *8·4*	3–6, *4·3*	5–10, *6·8* (19)
Metathor.	1	2–6, *3·7*	3–10, *6·9*	4–8, *6·0*	7–12, *8·6*	4–11, *6·9* (17)	6–12, *8·8* (13)
Abdom. I.	3	1–2, *1·3*	1–3, *2·6*	1–3, *1·8*	1–3, *1·6*	1–3, *1·3*	1–1, *1·0*
,, I.	9	4–6, *5·1*	3–7, *5·3*	5–7, *5·5*	4–6, *5·1*	2–5, *3·2*	4–6, *4·7* (13)
,, II.	13	5–10, *7·1*	4–8, *5·8*	3–7, *5·3*	3–5, *3·1*	3–7, *4·6*	3–5, *3·6*
,, III.	6	13–20, *16·4*	15–23, *18·6*	16–25, *19·3*	6–14, *9·2*	13–21, *15·7* (20)	15–25, *17·8* (13)
,, III.	9	7–12, *8·5*	6–11, *9·2*	7–12, *8·3*	5–7, *6·3*	3–9, *5·8*	5–7, *6·7*
,, IV.	6	2–3, *2·3*	2–3, *2·5*	2–3, *2·5*	3–5, *3·5*	1–3, *2·3* (20)	1–3, *2·2* (13)
,, IV.	9	7–11, *8·3*	7–12, *9·9*	8–10, *9·0*	4–7, *5·3*	5–9, *7·1*	5–7, *5·9*
,, IV.	13	3–4, *3·1*	4–7, *5·2*	3–5, *3·6*	2–3, *2·7*	3–6, *4·8*	1–2, *1·8* (13)
,, V.	6	2–3, *2·3*	1–3, *2·1*	2–3, *2·2*	2–4, *2·9*	1–3, *2·1* (20)	1–2, *1·7* (13)
Number of specimens		9	20	10	10	40	10

Means are in italic figures; number of specimens as given, unless otherwise shown in brackets.

TABLE XIII.—*Pupal chaetotaxy & T.-M. Index.*

Form.	Number of specimens.	III.C.	IV.C.	V.B.	T-M Index.
A. l. balabacensis :					
Borneo	10	7–13, *9·0*	5–9, *6·2*	5–10, *8·1*	0·82–0·91, *0·88*
N. Malaya	9	7–11, *9·0*	5–10, *6·6*	5–8, *6·8*	0·82–0·89, *0·85*
Balabac*	20	7–11, *8·3*	5–8, *6·4*	5–9, *6·8*	*0·80*
A. l. leucosphyrus:					
Borneo	10	5–13, *7·5*	3–8, *5·1*	4–7, *5·4*	0·80–0·95, *0·89*
Malaya	11	3–8, *5·5*	3–6, *4·5*	4–7, *5·8*	0·88–0·95, *0·92*
A. leucosphyrus :					
"Luzon form"*	15	4–8, *5·4*	3–4, *3·1*	3–5, *4·2*	0·75–0·79, 0·77†
"Negros form"	3	3–6, *4·5*	3–5, *3·4*	4–7, *5·7*	0·72–0·79, *0·75*
"Fraser's Hill form"	10	5–11, *8·2*	5–10, *6·3*	4–6, *4·9*	0·80–0·89, *0·84*
"Kepong form"	6	7–13, *10·0*	6–11, *9·0*	7–12, *8·6*	0·89–0·94, *0·92*
A. riparis macarthuri :					
Borneo	10	5–9, *6·9*	3–6, *4·4*	4–8, *6·0*	0·71–0·83, *0·77*
Malaya	10	4–9, *6·0*	3–6, *4·3*	5–10, *6·9*	0·75–0·84, *0·80*
*A. cristatus**	23	6–17, *8·7*	3–8, *5·3*	6–11, *8·7*	*0·70*
A. pujutensis	18	4–10, *5·8*	3–6, *4·4*	3–6, *4·8*	0·76–0·87, *0·83*
A. elegans	1	7·0	4·0	5·0	0·88
A. hackeri :					
Borneo	10	14–23, *16·6*	6–16, *9·9*	6–10, *7·5*	0·77–0·82, *0·79*
Malaya	3	7–12, *9·3*	4–8, *6·5*	4–9, *6·5*	0·79–0·83, *0·81*

Means are in italic figures.

* From Baisas (1936*a*); T.-M. indices estimated from illustration.
† From 2 specimens measured, and Baisas' illustration.

TABLE XIV.—*Mean lengths and ratios of pupal spines.*

Form.	Number of specimens.	Spine length, mm. III.A.	IV.A.	V.A.	Ratios. IV.A/III.A.	IV.A./V.A.
A. l. balabacensis :						
Borneo	10	0·020	0·076	0·099	3·12–6·00, *3·99*	0·67–0·86, *0·78*
N. Malaya	9	0·016	0·071	0·090	3·50–5·25, *4·40*	0·73–0·87, *0·79*
Balabac*	—	0·018	0·070	0·093	— , *3·80*	— , *0·75*
A. l. leucosphyrus :						
Borneo	10	0·014	0·032	0·094	1·50–3·33, *2·34*	0·21–0·52, *0·34*
Malaya	11	0·016	0·044	0·089	1·75–4·00, *2·29*	0·28–0·83, *0·44*
A. leucosphyrus :						
"Luzon form"*	—	0·011	0·018	0·056	— , *1·62*	— , *0·32*
"Negros form"	3	0·014	0·049	0·083	1·25–3·80, *2·83*	0·25–0·60, *0·48*
"Fraser's Hill form"	10	0·018	0·047	0·118	2·00–3·17, *2·61*	0·32–0·50, *0·40*
"Kepong form"	6	0·027	0·064	0·106	1·82–3·25, *2·63*	0·48–0·81, *0·65*
A. riparis macarthuri :						
Borneo	10	0·011	0·019	0·106	1·33–2·00, *1·68*	0·14–0·23, *0·18*
Malaya	10	0·011	0·019	0·107	1·00–4·00, *1·89*	0·11–0·27, *0·18*
*A. cristatus**	—	0·015	0·018	0·108	— , *1·28*	— *0·17*
A. pujutensis	18	0·016	0·024	0·084	1·00–1·80, *1·53*	0·18–0·40, *0·29*
A. elegans	1	0·016	0·033	0·115	— , *2·00*	— , *0·29*
A. hackeri :						
Borneo	10	0·013	0·018	0·128	1·17–1·75, *1·34*	0·10–0·18, *0·14*
Malaya	3	0·011	0·018	0·129	1·00–1·25, *1·17*	0·09–0·14, *0·12*

Means are in italic figures.

* From Baisas (1936*b*); ratios derived from mean lengths.

PART II. BIOLOGY.

1. Introduction.

Information concerning the biology of the various members of the *A. leucosphyrus* group, as in many others, varies in quantity in direct proportion with their importance as vectors of malaria. Thus a not inconsiderable amount is known about the widespread and dangerous *A. l. balabacensis*, somewhat less about *A. l. leucosphyrus* and very little concerning the others. Hence the following section deals mainly with *l. balabacensis* which has been investigated in some

Fig. 15.—Tentative boundaries of range of *A.* "*leucosphyrus*" (dotted line) and distribution of "monsoon forest" and "tropical rain forest" vegetation types (stippled; from Batholomew, 1947). Continuity across India, and the exclusion of Hainan Is.* and adjacent coast remain doubtful.

* I have since found a record of *A.* "*leucosphyrus*" from Hainan (Takei, 1941—not seen, but quoted by Chow, 1949).

detail in Borneo, Assam and Burma; also, to a lesser degree, with *l. leucosphyrus*.

Despite this general lack of information, it is clear that all members of the group share a common broad ecological niche, in that all are creatures of the tropical forests, extending from S.W. India, eastwards to Celebes and North to Yunnan[9], Formosa[10] and the Philippines. All are obligate haunters of primary and secondary forest, including man-made plantations, and are not to be found in open country; neither are they represented amongst the brackish-water

[9] Sweet, Feng, Chow and Hsu, 1942 (*A.* "*leucosphyrus*").
[10] Chang, Watson and Chow, 1950 (*A.* "*leucosphyrus*").

breeders of the tidal zone, though they may be found in fresh water sites in tidal zone forests.

To the east, their range is bounded by the zoo-geographic discontinuities of Wallace's and Weber's Lines, but otherwise the general distribution follows closely that of the " monsoon forest " and " tropical rain forest " vegetation types, as given by Bartholomew (1947) (*see* fig. 15) ; these in turn are limited to regions within the 60-inch isohyet and 60° January isotherm. Within this broad ecological zone the various species occupy individual niches, but all remain creatures of the forest, leaving its shelter rarely, and then only as adults in search of a blood meal.

2. Larval Breeding Places.

Although a mosquito's breeding place is determined largely, if not solely, by adult behaviour, the subject is most conveniently treated separately. The preferred breeding place is, in fact, the resultant of a balanced system of adult and larval biology, whereby the gravid female lays her eggs in sites favourable for larval development. As far as can be seen, in many species the limits are determined largely by adult behaviour, with the larvae showing a rather wide tolerance of breeding conditions, but there may be small and as yet undetected differences in adaptation to conditions in natural breeding places. From evolutionary theory it appears inevitable that mutal adaptations will appear in both adult and larval biology, limited only by the plasticity of the genotype.

In the case of *A. l. balabacensis*, as in many species, the breeding place possesses certain characteristic features, of which the ease of recognition by the trained observer is only equalled by the difficulty of accurate definition. The typical breeding place may be described as a small pool or group of pools, in a clay soil, containing fairly clean seepage or rainwater, still or with a barely perceptible flow, and under some degree of shade. Such conditions, however, may occur in a variety of situations and must be qualified with certain limitations as to general terrain, etc. Thus it should be added that there is a close association with hilly country and forest cover and that, in Borneo, the upper limit of altitude appears to be around 4,000 feet.

It is important to note that *balabacensis* is a *pool*-breeder, practically never found in streams or other running water, although it may occur in backwaters and residual pools in stream beds. The water in the pools is fairly clear or tinted brown by rotting leaves, but often shows a strong turbidity when stirred—strangely enough, the sparkling clear water of a certain type of jungle seepage appears to be unfavourable for breeding. In most pools the water is regularly or sporadically freshened by seepage or rain, and complete stagnation appears to be unfavourable ; under such conditions of regular freshening, pollution and disturbance by animals has little effect, on the larvae at any rate, and heavy breeding has been observed in pools heavily fouled by buffaloes.

Vegetation in and around the pools varies with situation, but in the more open sites the margin is commonly fringed with grass. In Borneo the carpet-grass, *Axanopus compressus* (Malay—rumput manis ; Dusun—telinting), is a useful indicator owing to its preference for soil and water conditions which favour breeding. In heavy forest there is no grass, but dead leaves accumulate in the

pools, staining the water a deep brown colour and appear to produce conditions particularly favourable for breeding.

The soil type around breeding pools is rather strongly characteristic since an overwhelming majority occur in a soft, sometimes sticky, yellow- to orange-brown clay, with a layer of fine clay silt on the bottom ; on stirring, this produces a strong and persistent turbidity. On dark alluvium or peaty soils breeding is rare. The characteristic clay silt is perhaps principally an indicator of water conditions, produced by steady seepage or gentle run-off, and is found in pockets in the hills or along the hillfoot or valley bottoms.

Shade conditions vary considerably, from the gloom of thickly overgrown jungle to the partial shade of a few tall trees. In general, breeding pools are shaded for at least a few hours during the heat of the day and direct sunlight throughout the period 9 a.m.–3 p.m. appears completely to inhibit breeding. In Borneo, breeding places are mostly found under moderate shade in, or along the edge of, fairly open jungle or plantations, but this is probably correlated with human and animal activity (*see below*). It should be stressed that, along the jungle margin, larvae may thrive in pools which receive shade for only a few hours over midday, and that from only one or two trees.

A point of considerable importance is that the heavy breeding which makes this species such a dangerous vector is commonly a result of human or animal activity. The soft marshy soil around seepages in jungle ravines and along the hillfoot rapidly becomes puddled by footprints of buffalo, pig, deer, man, etc., into areas of small, almost stagnant pools, highly favourable for breeding. Likewise, pools and wheelruts along tracks, blocked drains, shaded borrow-pits, pig- and buffalo-wallows, etc., all contribute a significant quota to the total of breeding places.

McArthur (1947) regards the virgin jungle seepage, hidden in dense, deeply-shaded forest, as the most important breeding place of *balabacensis*, but in the writer's opinion this is not so. Generally throughout Borneo the bulk of the larval population occurs in the more open and temporary situations—this agrees, moreover, with the published records from other countries, *e.g.* Reid (1949), Macan (1948), Kuitert and Hitchcock (1948). *A. l. balabacensis* is presumably originally a breeder in virgin jungle-seepages, but wherever man and domestic animals penetrate, increased breeding is wellnigh inevitable. This is probably the reason for the observation by Macan (1948) that military operations in the forest produce an increase in numbers of this species.

An interesting aspect of this situation was observed at Tambunan, North Borneo, in 1949, when breeding places were being eliminated by removal of shading vegetation. In several places breeding was found in hoofprints beneath trees where buffaloes congregated for shade. Removal of the trees eliminated the breeding places, but the animals simply shifted to adjacent sites and in a short time produced new breeding places. The surveys made during this same experiment also demonstrated the relative impermanence of many breeding places—of some 300 found in an initial survey, 50 were found to be dry or negative for *balabacensis* during a re-survey about one month later. Moreover, this latter survey revealed 85 new breeding places, most of which had been examined and found negative previously.

In North Borneo, there is a marked association between hilly country and *A. l. balabacensis*, to such an extent that one tends to regard any hilly area as

malarious and flat land (away from the coast) as healthy. The correlation is apparently due to the fact that the hills are usually covered with jungle and that the soil and water conditions which favour breeding occur mainly in the hills. But some notable exceptions are found—the town of Limbang, Sarawak, situated at the foot of a jungle-covered ridge, is nevertheless virtually free of malaria, simply because slopes are too steep and the soil too permeable to form breeding pools. Conversely, a few miles from the town, a small pocket of malaria occurs on apparently flat alluvial plain ; here breeding places occur around a small residual " hogsback " of yellow clay, only some 10 feet high and covering about one acre.

Generally, *A. l. balabacensis* displays considerable plasticity in its choice of breeding place within the limits described. Despite its usual occurrence in these situations, it has also been found occasionally, by the writer and others (McArthur 1948 ; Kuitert and Hitchcock, 1948), breeding at swamp edges, or in rock-pools, bamboo stumps, split bamboos, and tins and other artificial containers. Such breeding places must, however, be regarded as adventitious and rare.

As regards other members of the group, *A. l. leucosphyrus* (Doorenbos, 1931 ; Colless, 1954), the " Celebes form " (van Hell, 1952) and *A. pujutensis* seem to resemble *balabacensis* in choice of breeding place and show the same rather elastic behaviour. In Borneo and Malaya *pujutensis* is commonly found associated with, and even in the same pool as, *l. leucosphyrus* or *l. balabacensis*. It shows certain peculiarities, however, in that it has not been found in the hilly interior of North Borneo, though it does occur in the less elevated interior of Sarawak (Colless, 1954). Moreover, around Miri, Sarawak, it is the dominant form of the group, *balabacensis* being very rare. Whether this distribution is determined by availability of breeding places is, however, not clear.

Available records of the *A. riparis* subspecies (Baisas, 1936*a* ; Reid, 1949 ; Colless, 1954) indicate a clear-cut preference for breeding in rock-pools along heavily shaded streams or amongst gravels at their edges. The related *A. cristatus* is also a rock-pool breeder, but may also occur in tree holes (Baisas, 1936*a*.). *A. hackeri* is closely restricted to collections of rain-water in bamboo stumps and split bamboos, and open tree holes ; also (Institute for Medical Research, 1951) between the old leaf-bases of Nipah palms. *A. elegans* is, as far as known, a breeder in shaded ground pools, but I have seen a number of specimens collected from rock-pools and holes in tree—and bamboo stumps in Ceylon—whether this type of breeding place is common is unknown.

Effects of clearing on breeding places of A. l. balabacensis.

During experiments carried out at Tambunan, North Borneo, in 1949, it was found that breeding places of *A. balabacensis* could be almost completely eliminated by removal of shading vegetation (McArthur, 1954). The admission of direct sunlight to the breeding pools throughout the period 9 a.m.–3 p.m. appeared to be sufficient and, in treated breeding places, the degree of control was estimated to be more than 90 per cent.

The results of larval surveys, made before and after clearing, have been analysed to gain some idea of how such control operates, with rather interesting results. Table XV below shows the survey results, as number of larvae per 10

minutes collecting, from 33 breeding places which were regularly re-surveyed for almost three months after clearing.

TABLE XV.—*Larval numbers before and after clearing.*

Period after clearing.	*A. l. balabacensis*		*A. kochi*		*A. maculatus*		Other spp.		
	No.	Per cent. of total.	No.	Per cent. of total.	No.	Per cent. of total.	No.	Per cent. of total.	Total. No.
Pre-clearing	10·5	90·5	0·9	8·0	0·2	1·5	0	0	11·6
2– 3 weeks	15·7	59·8	3·2	12·3	7·1	27·0	0·2	0·9	26·2
5– 6 ,,	10·9	47·8	1·5	6·4	10·4	45·4	0·1	0·4	22·9
10–11 ,,	1·3	8·1	0·4	2·5	14·0	89·0	0·1	0·4	15·8

It had been assumed beforehand that any success in control would result from a direct effect of increased light and exposure upon the ovipositing female, but the figures quoted show that such an hypothesis is untenable. The inhibiting factor is obviously one which builds up slowly with time, to favour the "sun-loving" *A. maculatus* at the expense of *A. l. balabacensis*, and must be some *indirect* effect of the clearing process. The gradual decrease in larval numbers is well shown in the figures below from two breeding places, cleared on 19th June and regularly re-surveyed ; the figures given are numbers of *balabacensis* larvae per 10 minutes collecting.

	17th June.	21st June.	26th June.	3rd July.	13th July.	21st July.
Breeding place 1 .	25	39	29	9	6	7
,, ,, 2 .	34	30	30	24	16	14

During this gradual decrease there was no indication whatever of increased larval mortality—the ratio of third instar to fourth instar remained approximately constant, and healthy mature larvae and pupae were found even when breeding had reached a very low level. The inhibitory effect was obviously acting against the ovipositing female.

Visual examination of numerous breeding places showed no macroscopic changes which might be producing the inhibitory effect, nor did tests of pH show any significant changes. Within a few days of clearing, however, there was a rapid build-up of a brown, oil-like scum of iron-bacteria on the pools, but this was rapidly transitory and uncorrelated with the gradual disappearance of *balabacensis* larvae. Moreover, a complete cover of the scum inhibited *all* species.

The slow build-up of the inhibiting factor(s) seems most likely to be correlated with gradual change in the physico-chemical, or biological characters of the water ; such as might result from an altered micro-flora and fauna, or changes in the processes of decomposition of organic matter, etc. The rapid increase in bacterial scum may indicate the onset of such changes, or help to produce them, and the general picture tends to agree with the observed tendency for completely stagnant water to be unfavourable for breeding. However, the actual nature of the postulated factor(s) remains completely obscure.

Larval habits and biology.

The larva of *A. l. balabacensis* has been described by McArthur (1948) as very elusive and difficult to find during surveys, owing to inaccessibility of breeding places and a tendency to remain submerged for long periods. In the writer's experience this elusiveness is not apparent if one is fortunate enough to commence with a suitable technique of survey. First, it is essential to examine a sufficiently large sample of the numerous small pools found around seepages, paying particular attention to those nearest the hill foot. Second, the larvae, when disturbed briefly and suddenly, usually rise rapidly to the surface, but if disturbed a second time, dive and may remain submerged for up to about one minute; subsequent disturbances have an even more marked effect and some larvae may, as described by McArthur (*op. cit.*), cling to the bottom for up to five minutes. Thus, when searching for *balabacensis*, the pools should be rapidly stirred for only several seconds, or the water lifted cleanly and suddenly in a scoop and the larvae collected with a pipette as they break the surface. Using this technique, collection is rapid, simple and complete.

McArthur (*op. cit.*) has also described several preliminary experiments which suggest that light and pH conditions play a part in limiting the breeding places of *balabacensis*, by a direct lethal effect on the larvae. As regards pH, the writer could find no evidence of such an effect in the Tambunan area of North Borneo; 31 breeding pools were tested, using brom-thymol blue and a comparator, and showed a range of 6·0–7·2, with no obvious preference in the range 6·0–7·0. Many other pools, negative for *balabacensis*, showed this same range and, in fact, almost all ground water, with the exception of the lower reaches of streams, showed a pH of 6·0–7·2. The experimental mortality recorded by McArthur appears to have been due to rapid transition of mature larvae from acid to alkaline media, and it is doubtful if, in nature, pH plays any role whatsoever.

As regards the effects of direct sunlight, no further experiments have been made with *balabacensis*, but it has been observed that in cleared breeding places healthy larvae may be found in pools open to direct sunlight and with a negligible amount of shade afforded by the edges or fringing vegetation. As regards the related *A. pujutensis*, which has virtually identical shade requirements, an experiment was made to test the effects of sunlight alone, while preventing any concomitant rise in water temperature. Thirty larvae were placed in a petri dish of water, which was floated on the surface of a large container through which water flowed constantly; the current of water kept the petri dish in motion and agitated its contents. Exposure of the apparatus to four hours of morning and midday sunlight produced no mortality in the larvae, while a smaller batch, similarly exposed but without cooling, were all killed. The lethal effect appears then to be due to the heating effect of the sun's rays. Presumably in at least some natural breeding pools, seepage flow and conduction can keep temperatures below lethal levels.

In the laboratory, larvae of *A. l. balabacensis*, *A. l. leucosphyrus*, *A. riparis macarthuri*, *A. pujutensis* and *A. hackeri* have all proved easy to rear, using small bowls of six inches diameter, and a medium of tap- or stream-water and "Farex" (a proprietary brand of baby-food); dead insects are also a useful emergency food, and a layer of soil on the bottom of the bowl is also useful. Quite considerable departures from this technique have indicated that all these forms are relatively

insensitive to changes in the breeding water, provided that such are made gradually.

3. Adult biology.

(a) *Outdoor resting places.*

All observations show that members of the *leucosphyrus* group are " wild " species, in the sense that they are rarely, if ever, found resting by day inside human dwellings. Engorged females of *A. l. balabacensis* and *A. l. leucosphyrus* are sometimes found trapped in defective mosquito nets, while the writer (Colless, 1954) records several specimens of the latter subspecies taken by day in a dark cubicle in a longhouse. It is clear, however, that the normal resting place of all forms is out of doors, as is the case with most mosquitoes of Malaysia. There is, however, the puzzling record by Stoker (1934) of 53 *A.* " *leucosphyrus* " taken by day (" overdag, in huizen ") on Pulau Laut. These were, presumably, one of the *A. leucosphyrus* subspecies and, unless they were taken from defective nets (the number seems rather high for this), this record constitutes a remarkable exception to general behaviour.

Searches were made in North Borneo by the writer for outdoor resting places of *A. l. balabacensis*, and on Labuan Is. several places were found where this and other species could be taken regularly. The first and most productive place was near a house in an old plantation of rubber plus a few coconut palms, with an almost complete overhead canopy. The undergrowth was being cleared and resting adults were found amongst the loose heaps of cut vegetation ; other species, particularly *A. philippinensis* and *A. kochi*, were also common amongst the low uncleared undergrowth, but *balabacensis* was not found in such sites. In this area some five adults, male and female, of *balabacensis* could be collected per man/hour. The second site, once again near a house, was a patch of dense secondary jungle, fringed by marshy soil with tall sedge. Here collecting was exceedingly tedious and yielded only 2–3 per man/hour, but many escaped. In all cases, the adults were resting in well-sheltered, moist places, on living or dead vegetation, up to about one foot from the ground and in subdued light (very dark places seemed to be avoided). Females thus taken were in all stages of ovarian development and one had sporozoites in the salivary glands. A further two females were taken in similar sites in secondary jungle at Tambunan, and McArthur (1948) records a further six taken previously in a similar fashion in the same area. The records of Kuitert and Hitchcock (1948) from Burma, also imply that many of their specimens (presumed to be *balabacensis*) were taken from outdoor sites similar to those described above.

Searches of open areas adjacent to these sites proved uniformly negative. Careful attention to banana plants and the surrounding litter, and similar likely places around houses, yielded no specimen of *balabacensis* and it seems safe to conclude that this form normally rests by day out of doors, in moist shaded sites in jungle or similarly protected places. It should be noted, however, that *balabacensis* has an effective flight range of about half a mile *away from jungle* (Colless, 1953*a*). It seems inconceivable that all females feeding at such a distance from the jungle margin could make the return journey in a single bound, and it is therefore likely that a limited amount of resting takes place in sheltered sites outside the jungle.

As regards other members of the group, it seems likely that their resting habits are much the same as those of *l. balabacensis*. Wharton (1950) records a single specimen of "*leucosphyrus*" (probably the type-form) from the banks of a stream in a Malayan rubber plantation, while it is reported, also from Malaya (Institute for Medical Research, 1951), that *A. pujutensis* and *A. hackeri* were found in some numbers in crevices at the bases of Nipah palms.

(b) *Flight and feeding habits.*

A. l. balabacensis. The nocturnal activity of *l. balabacensis* has been examined in some detail by McArthur (1947, 1948), Macan (1948), and the writer (Colless, 1952), and further observations are given below. All agree that this form is a late-feeder with a peak of activity in the early hours of the morning. In North Borneo, feeding usually commences between 8 p.m. and 9 p.m. and continues until daybreak, and on individual nights the peak may vary from as early as 10–11 p.m. to as late as 4–5 a.m. Over a period, however, the bulk of the catch is taken between midnight and 4 a.m. This is illustrated in figure 16, by the results of nine all-night catches from Labuan Is., and figure 17, from Tambunan, the latter taken from McArthur (1948).

Records of temperature, humidity and weather were kept during the Labuan Is. catches, but offer no explanation of the form of the feeding-cycle, and, as pointed out by Haddow (1954) for African species, it is unlikely that the observed behaviour is conditioned at all by microclimate. Haddow (*op. cit.*) has further shown that, in *Aedes longipalpis*, the regular curve of the biting cycle is actually the resultant of a series of bi-modal curves, and some such situation may prevail in the case of *l. balabacensis* also. It has been shown (Colless, 1953*b*) that in houses treated with DDT and kerosene the feeding cycle of this form becomes bi-modal with an abnormally early first peak. Also, records of the individual nights grouped in figure 16 suggest that a bimodal curve may sometimes occur, and figure 16 shows a possibly significant drop in the 2–3 a.m. period. Haddow suggests that such bi-modal cycles may be produced by separate groups of the population feeding at different times, perhaps the older mosquitoes and the nulliparae. In this regard, dissections of large numbers of *balabacensis* in North Borneo showed that almost all females taken feeding were fertilised and in ovarian stage 2; but many catches made between 8 and 11 p.m. contained old mosquitoes, as indicated by the presence of individuals with sporozoites in the glands. Such flimsy evidence cannot be laboured further, but if such a division of the population does occur, it is likely that the earlier arrivals are the older mosquitoes.

Observations made outside houses on Labuan Is. shed further light on the mosquitoes' movements during the biting cycle. Early in the night, from about 9 a.m. onwards, unfed females could be found resting on the piles and outside walls and in nearby foliage, with a marked tendency to congregate in the near vicinity of the house. It is clear that a considerable proportion of the population emerges and arrives at the house quite early in the night and spends a significant period resting outside before entering to feed. Moreover, when catches are made out of doors the same situation is observed, indicating that this resting period is not due to any "unwillingness" to enter the house, but that the mosquitoes are insufficiently activated for feeding to occur. The length of this resting

period has not been accurately estimated, but has been observed to last for over two hours in some cases.

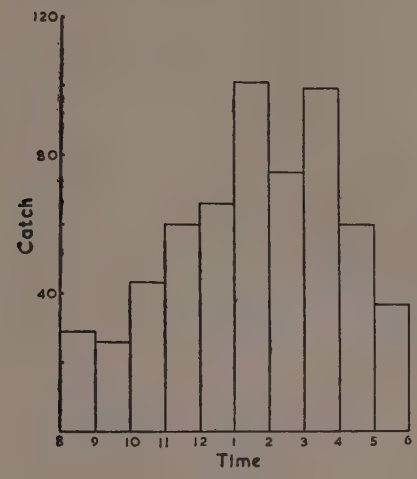

Fig. 16.—Total catch of *A. l. balabacensis* by hourly periods, nine nights, Labuan Is.

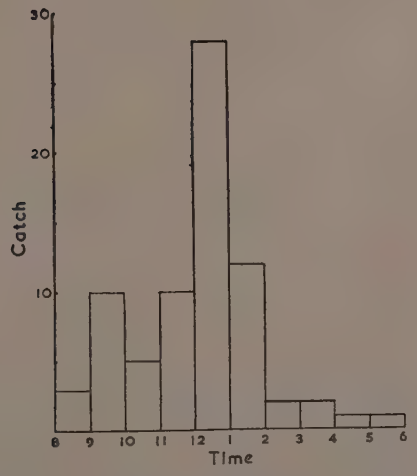

Fig. 17.—Total catch of *A. l. balabacensis* by hourly periods, Tambunan (from McArthur, 1948).

As regards entry into houses, Table XVI below gives the results of three catches made on Labuan Is., during which mosquitoes feeding on human bait were collected simultaneously inside and outside the house.

TABLE XVI.—*Comparative catches, inside and outside house.*

Species.	*A. l. balabacensis.*	*A. philippinensis.*	*A. kochi.*	*A. tesselatus.*
Outside . .	30	48	15	9
Inside . . .	24	2	2	0

It is clear that *balabacensis* is little, if at all, averse to entering houses, in marked contrast to the other three species.

Once inside the house, observations show that many mosquitoes rest on the walls, both before and after feeding. During one night, in November 1949, careful observations were made of individual females of *balabacensis* in a house on Labuan Is., with the following results :

Seen to rest before feeding—14 ; resting period 0–78 mins., av. 14 mins.
Seen to feed—25.
Seen to rest after feeding—30 ; resting period 0–182 mins., av. 49 mins.

Thus, of 30 mosquitoes which fed (five unnoticed), 14 or 47 per cent. rested before feeding and all rested after feeding. Engorged females rested some three to four times as long as those unfed, in some cases for over three hours.

During a subsequent series of observations, made over a period of one month (seven all-night catches), the following results were obtained :—

Rested before feeding . . .	28
,, after feeding	67

All which were seen to feed rested on the walls afterwards and the proportions were much the same as in the previous results. The average periods of rest are given below in Table XVII, grouped into two-hourly periods ; individuals were allotted to the period in which most of their resting period fell.

TABLE XVII.—*Average periods of rest on walls (minutes).*

	Unfed.		Fed.	
Time.	Number.	Av. resting period.	Number.	Av. resting period.
8–10 p.m.	4	5·0	10	23·5
10–12 p.m.	9	3·4	17	19·9
12– 2 a.m.	6	3·7	17	28·2
2– 4 a.m.	7	3·0	15	60·7
4– 6 a.m.	2	1·5	8	74·9

With unfed mosquitoes the resting period did not vary greatly throughout the night though it was considerably less than that recorded above in the first set of observations ; there is some suggestion of a steady decrease throughout the night, but the numbers are too small to give any great degree of accuracy. In the case of fed mosquitoes, however, there is clear evidence that the resting period increases throughout the night, reaching a maximum between 4 and 6

a.m.; this despite the fact that some individuals had their resting period curtailed by the advent of daylight. Resting periods of more than one hour were only observed in the 2–4 a.m. and 4–6 a.m. periods (8 out of 15 and 5 out of 8, respectively).

Haddow (1954) has drawn attention to the curious tendency of many species to attack the bait in successive waves at short intervals—probably most observers have noticed this common phenomenon, which is well illustrated by

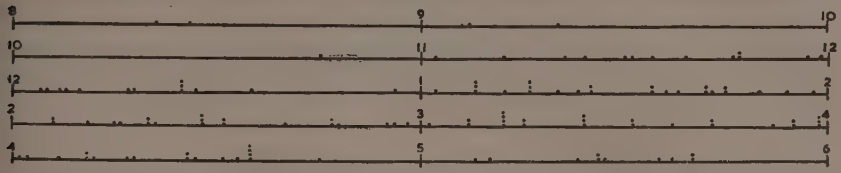

FIG. 18.—Individual biting times of *A. l. balabacensis* in a single night, Labuan Is. Times are to the nearest minute and read from left to right, top to bottom; each dot represents a single capture.

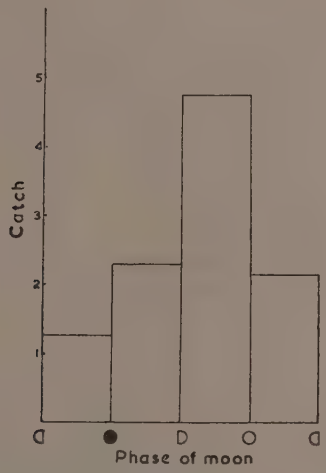

FIG. 19.—Average nightly catch per man, of *A. l. balabacensis*, according to phase of moon, Labuan Is.

l, balabacensis. Figure 18 shows the actual biting times of 135 individual mosquitoes caught during a single night on Labuan Is. The tendency to arrive in waves is obvious, and no cause could be found in atmospheric conditions.

A further interesting feature of catches made on Labuan Is. was a marked correlation between feeding activity outside houses and incidence of moonlight. During July-November 1948, regular, almost nightly, catches were made between 8 and 11 p.m. outside houses or, occasionally, on an open verandah. Analysis of these catches according to phase of moon is shown in figure 19, where it can be seen that the maximum falls in the period first quarter to full

moon, *i.e.* the period when moonlight was potentially available throughout the catching period. The minimum falls in the period last quarter–new moon, with no moonlight before midnight, and during intermediate periods, intermediate catches were recorded. There is thus a strong suggestion that moonlight has an activating effect on feeding out-of-doors. Unfortunately, available information is insufficient to show whether the time of the feeding-peak is affected by moonlight (as shown for *A. funestus* by Ribbands, 1946), and what effect, if any, is produced inside houses. The writer (Colless, 1953*b*) has shown that in houses treated with DDT and kerosene, moonlight has no effect on behaviour, but this could be due to the presence of the insecticide and its solvent, both of which affect behaviour.

Other forms.

Little is known of the nocturnal activity of other members of the group, with the exception of *A. l. leucosphyrus* in Sarawak. With regard to the latter, observations by the writer (Colless, 1954) show that its behaviour is virtually identical with that of *balabacensis* in North Borneo. There is the same build-up of unfed mosquitoes outside the house, with resting periods of up to several hours, the same late feeding peak after midnight, and the same tendency to rest on walls. Also observed was a tendency to enter earlier and rest longer before feeding during wet weather, and a tendency for unfed mosquitoes to rest on walls to a progressively decreasing extent later in the night; these points have not been investigated for *balabacensis*. Also of interest is the fact that phase of moon showed no effect on the biting cycle indoors, which suggests that the same is true of *balabacensis*.

Factors determining the feeding cycle.

In a recent paper on *A. l. leucosphyrus*, the writer (Colless, 1954) essayed briefly to connect together the known facts of its feeding cycle, and so to give some picture of the pattern of stimulus and response which guides the female through this characteristic behaviour. Since *A. l. balabacensis* appears to possess a virtually identical feeding cycle, it is legitimate to pool what is known of the two subspecies and consider the matter in more detail. In addition to the facts already noted, further relevant information is provided by the effects of DDT and kerosene upon resting mosquitoes since it has been shown (Colless, 1953*b*) that in *l. balabacensis* these substances may stimulate the mosquito to perform the next act in the cycle, *i.e.* if unfed it proceeds to feed, if fed it flies out. Kerosene vapour also appears to produce an abnormal cycle with early and late peaks.

Considering first movements outside the house, there is the question of the stimulus which initiates flight activity and brings a nocturnal mosquito out from its daytime resting place. Lumsden (1952) and Haddow (1954) have suggested that, in some species at least, this initial stimulus is actually a " release " of the inhibiting effects of light. This attractive hypothesis agrees with the frequently-observed activation of caged mosquitoes, during a sudden reduction of light, *e.g.* Muirhead-Thomson (1941) for *A. minimus*. This same effect has been noted in caged, unfed females of *balabacensis* and the initial stimulus in *A. leucosphyrus* may well be a release of such restraining factors. The stimuli

operating later in the feeding cycle may also involve " releases " of this nature and the term " activation", as here used, must be understood to include these, as well as positive stimuli.

Once the mosquito is thus activated there remains the much-neglected problem of how she is attracted to the vicinity of the bait. There is a tacit assumption throughout the literature that the mosquito actually searches for her victim and can detect it from considerable distances ; only one paper has been seen which deals specifically with this point (Ribbands, 1949) and its conclusions are discussed below. A number of workers, however, have tested short-range attractants, *e.g.* Reuter (1936), van Thiel (1937), Willis (1947), Mer, Birnbaum, and Aioub (1947), Parker (1949), Brown, Sarkaria, and Thompson (1951), Sippell and Brown (1953) ; although some results are contradictory, it does appear that, for certain species, warmth and moisture, and possibly CO_2 and the odour of sweat are the main attractants which bring the hungry mosquito to feed on the bait, and certain visual attractants have also been described. It is, however, most difficult to believe that such attractants, emanating from, say, a single animal, could establish detectable gradients over a distance of more than a few yards, or tens of yards, and such an effect seems totally inadequate to explain the feeding of *A. l. balabacensis* in houses up to half a mile away from its normal jungle habitat.

This problem is, however, more apparent than real, since there is no actual need to invoke the agency of long-range attractants. Once activated, the mosquitoes may fly at random, or orientated by wind-currents, temperature gradients, visual factors, etc., until they come to the immediate vicinity of the bait and thus within range of its attractant vapours. Ribbands (1949) has already suggested that many Anophelines reach the dwelling-place of the host by random wandering, but interprets his results as demonstrating a long-range attraction as well. Examination of his figures shows that they can be interpreted equally well as the result of random wandering plus short-range attraction. For instance, the more or less proportional increase of catch with amount of bait (up to three persons) could illustrate the short-range effect only. Also, it is shown that huts remaining in an otherwise destroyed village showed only a 20–50 per cent. increase in catches, instead of an expected tenfold increase ; but such a tenfold increase *postulates* an attraction effective over several hundreds of yards, and the much smaller increase cannot then be said to demonstrate such an attraction. It does, in fact, demonstrate that the degree of competition between the remaining huts and those removed was slight, as would be expected if attraction by the bait operated over a short range only.

In the case of the *leucosphyrus* subspecies the hypothesis of short-range attraction would also explain the observed tendency to rest near the bait before feeding. If the mosquito has been approaching the bait under the influence of long-range attractants it is difficult to see why it does not proceed direct to its goal—it has been shown above that there is little aversion to entering houses and that such resting occurs when the bait is out-of-doors as well as inside. An alternative and simpler hypothesis is that this initial resting period represents the *initial* contact of the mosquito with the vapours, etc., emanating from its bait, which produces a temporary deactivation or " fixation "; this could be produced by the balancing-out of attractant and repellent features of the complex environment close to the bait. However, long-range attraction is not

completely ruled-out, since it is still possible that the repellent, or deactivating, factors operate only at short range, or even that attractant factors become deactivating at high concentration. Either would explain the observed resting-period, but on other grounds neither seems very satisfactory.

Whatever the true explanation, it is clear that an initial deactivation does occur when the mosquito arrives near to the bait and that a period of time is required during which attractant stimuli build up the level of activation required to initiate the act of feeding. This may involve another " release " of the inhibiting effect of repellent features of the bait-environment. Direct observation suggests that the deactivating effect produces a " zone of fixation " with a radius of the order of 50 feet around a house containing some 5–10 persons. It is, perhaps, significant that *high* concentrations of unfed resting mosquitoes have only been observed around small houses with relatively few persons (*e.g.* Colless, 1954). Around a large longhouse with 200–300 occupants, resting adults were always sparsely scattered and difficult to find, due perhaps to a much wider " zone of fixation."

It is not clear whether the unfed mosquitoes found resting on walls *inside* the house are resting for the first time or whether there is a progressive shift across the " zone of fixation "—possibly both are true. In any case, an explanation is now seen of the tendency for unfed *l. leucosphyrus* to rest less upon inside walls as the night progresses. This follows from the fact that the later arrivals will include an increasingly greater proportion of individuals who have passed much of their pre-prandial resting period outside, further from the bait but within range of its attractant factors. Of those entering the house, both the proportion of fully activated individuals and the degree of general activation may be expected to increase throughout part of the night at least. The apparent decrease in resting period suggested by Table XVII may also illustrate this effect.

The foregoing hypothesis also explains the observed tendency of *A. l. leucosphyrus* to enter houses earlier, and rest unfed upon the walls to a greater extent, during wet weather. It is not clear just what factor promotes the early entry, but possibly the mechanical disturbance of outdoor resting places breaks the initial deactivation and promotes earlier approach. But it is clear that mosquitoes which have been " driven " inside in any such fashion must spend more time resting there before attaining the level of activation required for feeding.

Once this level of activation is acquired, during the period of rest outside and/or inside, feeding takes place, the approach to the bait being orientated by such short-range attractants as mentioned above (warmth, moisture, CO_2, etc.). Then, having fed, the mosquito usually leaves the host rapidly, to rest on the wall (or foliage, etc., if feeding outside), This may involve a release of the repellent features of the bait in which mechanical disturbance by movement probably plays a large part ; on a perfectly still bait engorged mosquitoes have been seen occasionally to rest for several minutes on the skin. Once on the wall or foliage, however, the engorged mosquito must pass a further, and longer, period of rest before a third activation occurs, that which allows, or causes, exit from the house. This reversal of behaviour suggests that physiological changes are produced by engorgement, tending to inhibit the attractiveness of the bait and thus enhance its repellancy. It is equally possible that the engorged mosquito

becomes indifferent to stimuli from the bait and must rest until a general type of activation is acquired which releases an attraction to the dim, but discernibly brighter, light outside.

There remains the observation (Table XVII) that fed mosquitoes rest for a progressively longer period later in the night. This would indicate that, for the fed mosquito, activating stimuli become relatively weaker, in strength or effect, as the night progresses. Since it seems unlikely that the change occurs in the stimuli themselves, the effect is probably a result of tiring of the reflexes which produce general flight activity.

Once out-of-doors little is known of the mosquitoes' movements. Occasional engorged specimens have been found resting outside, near a house, but these were possibly driven out by disturbances in the house, before becoming fully activated for outside activity. By sunrise, however, all have returned to their outdoor resting places, presumably owing to the repellent effect of strong light.

It is of interest to note that moderate doses of repellent or activating substances, such as DDT and kerosene, tend to break the deactivation, either before or after feeding, and promote immediate feeding or exit respectively. Observation suggests that even mechanical disturbance, *e.g.* by the light of a torch, has a similar effect. It seems fairly clear from the observations reported (Colless 1953*b*) that unfed mosquitoes must first have acquired some orientation towards the bait, and that the artificial stimuli must be relatively weak, if feeding is to follow. But it does appear that resting mosquitoes acquire a potential orientation to or from the bait before the stimuli involved can produce the degree of activation necessary for flight. This in turn suggests an explanation for the tendency to arrive at the bait in successive waves. Any slight local disturbances, such as movement of persons, puffs of wind, etc., would tend to release, as a group, those mosquitoes in the immediate vicinity which had acquired orientation but which were not yet fully activated ; the observed wave-effect could then follow.

The actual shape of the graph of feeding activity will, by the above hypotheses, be the resultant of two functions—the cycle of arrival in the vicinity of the bait and the distribution of individual activation times required to produce feeding. The cycle of arrival near the bait will likewise involve individual activation times to promote flight activity and the original spatial distribution of the mosquitoes. Since we have no quantitative data regarding these factors further speculation is not warranted, but it is obvious that mathematical models can be constructed to fit the observed results.

The course of events suggested above is, of course, highly tentative, but it is hoped that this outline may stimulate, and perhaps provide some basis for, further investigations.

(c) *Host preferences.*

When working with " wild " species, which rest by day in forest, it is extremely difficult to obtain engorged females in sufficient numbers for valid precipitin tests to be made. Hence such evidence of blood preferences is almost completely lacking in the *leucosphyrus* group. A number of authors (McArthur, 1948 ; Ramsay *et. al.*, 1936 ; Walch 1942) report the results of precipitin tests, but their material was all colllected inside houses, which inevitably introduces a strong bias.

However, the evidence of comparative trapping on different baits can be equally useful, and, from such trapping, it is clear that *A. l. balabacensis* has a strong preference for human blood. McArthur (1948) estimated that, in Tambunan, North Borneo, some 80–90 per cent. of the *l. balabacensis* population feeds on human blood, and the writer's experience amply confirms this statement. Exact figures are not available (except for the few recorded by Colless, 1948), but searches have been made on numerous occasions on and around tethered buffaloes, pig-pens, fowl-houses, etc., and on some four occasions only were specimens of *balabacensis* found. Moreover, during these searches human baits nearby were being freely attacked. Several specimens were taken which had apparently fed on tethered buffaloes, but the proportion which normally do so must be very low. Ramsay *et al.* (1936) in Assam found that, in the presence of numerous cattle, only some 20 per cent. of *A.* " *leucosphyrus* " fed on these, the remainder taking human blood. In unpopulated areas, of course, some alternative host must be available, probably monkeys—the preferences of *A. hackeri* and *A. pujutensis* (see below) are perhaps suggestive in this regard.

In the case of *A. l. leucosphyrus*, the record by Walch (1942) suggests a similar preference for human blood, which is confirmed by the writer's experience in Sarawak (Colless, 1954). Similarly, the " Celebes form " is known to feed on human blood, and its occurrence as a malaria vector suggests a distinct preference (van Hell, 1952).

As regards other forms, a limited amount of information from Malaya (Institute for Medical Research, 1951) suggests that *A. hackeri* and *A. pujutensis* feed above ground level, on monkeys. In Borneo, in places where the latter species was breeding in large numbers, a variety of baits have been searched without recovering a single specimen. It seems likely, then, that there too this species feeds on some unknown host, perhaps monkeys, above ground level. Reid (1949) mentions the possibility that several specimens of *pujutensis*, collected by Roper in North Borneo in 1913, were captured in mosquito nets, but in the writer's opinion this is most unlikely.

By courtesy of Mr. Reid I have seen two specimens of *A. leucosphyrus*, " Kepong form," taken with human bait in Malaya and it seems probable that all the *A. leucosphyrus* subspecies will attack man. *A. riparis*, however, in both Sarawak and Malaya shows a complete indifference or aversion to human baits. Although common in areas where trapping has been carried out, there is as yet no record of this species ever being taken with any bait whatsoever. In Sarawak the writer has searched human, pig, dog and fowl baits in the vicinity of breeding grounds with completely negative results, and it is clear that the preferred host is some creature of the forest.

(d) *Seasonal variation.*

It has been shown (Colless, 1952) that on Labuan Is., adult densities of *A. l. balabacensis* are closely correlated with rainfall. In the period examined, monthly catches were at a peak in July and reached their lowest point during the January-February dry season ; the correlation coefficient between catch and rainfall was around + 0·8. Such an effect clearly depends, in part at least, upon the nature of the breeding place. Wet weather causes a considerable increase in the area of puddled seepages, and in the number of adventitious ground pools available, unless falls are very heavy, when flushing may cause a

temporary decrease in breeding. Conversely, during dry weather, small pools dry out and seepages are reduced to small flowing channels. Macan (1948) records a similar situation with *l. balabacensis* in Burma.

It has been shown, however, by the writer (*op. cit.*) that the increase in adult numbers during wet weather is possibly also an effect of increased adult longevity, due to higher humidities. This is deduced from the close correlation found between adult numbers (and hence rainfall also) and sporozoite *rate* (coefficient + 0·83). The dissection results of Clark and Choudhury (1941) from Assam show a similar trend, and the results of Macan (1948) are also suggestive; the phenomenon is probably quite widespread and not confined to *A. l. balabacensis*. It should be noted also that catches of *A. l. leucosphyrus* in Sarawak (Colless, 1954) tend to rise immediately during wet weather.

It seems probable, then, that wherever found, seasonal fluctuations in these two forms and others of similar habits are determined largely by rainfall, with the proviso that temperature may also play a part in more northerly regions.

4. Vector species.

Three members of the group have been definitely incriminated as vectors of malaria, *A. l. balabacensis*, *A. l. leucosphyrus*, and the " Celebes form," and McArthur (1951) has given a complete summary of results to that date. The writer (Colless, 1950) has since shown that the vector form of North Borneo, incriminated by McArthur (1947), is actually *A. l. balabacensis*, and the known distribution of members of the group makes it almost certain that this form is also the *A.* " *leucosphyrus* " incriminated by Kuitert and Hitchcock (1948) and Macan (1948) in Burma, by Clark and Choudhury (1941) and others in Assam, and by Toumanoff, Morin, and others (summarised in McArthur, 1951) in Indo-China. Specimens have been seen which were actually collected by three of the above investigators (Macan, Kuitert, and Morin).

As regards the type-form, *A. l. leucosphyrus*, this has been definitely incriminated as the principal vector in the interior of northern Sarawak (Zulueta and Colless, unpublished) and is almost certainly the *A.* " *leucosphyrus* " incriminated by Bais (1920), Schüffner (1923), Doorenbos (1925) and others, in Sumatra. From distribution records it seems probable that this was also the form found infected in eastern Borneo by Goelarso (1934). The infections recorded from Pulau Laut by Stoker (1934) also refer to this form or *l. balabacensis*.

Recorded incriminations of " *A. hackeri* " from Celebes almost certainly refer to the " Celebes form," as is clear from the work of van Hell (1952, and personal communication), but its actual importance as a malaria vector is not yet clear. It is obvious, however, that all the above forms must be regarded with suspicion wherever they occur, and the occurrence of *l. balabacensis* in the S. Philippines, the Andaman Is., N. Malaya, W. India, and parts of Java, suggests that there may remain areas where its importance has not yet been recognised. However, its potency as a malaria vector may perhaps vary considerably with local conditions, as is the case with *l. leucosphyrus*, which appears to be harmless in Malaya due to its relative rarity.

As regards other members of the group, no suspicion has yet fallen on them and *A. pujutensis*, *A. riparis* and *A. hackeri* must be regarded as definitely harmless, owing to their preference for hosts other than man.

5. Summary.

(1) *A.* " *leucosphyrus* " is distributed throughout South-East Asia, from W. India, north to Yunnan and Formosa, and east to Celebes. Its range is limited to the east by the Wallace and Weber lines, but otherwise coincides closely with the " monsoon forest " and " tropical rain forest " vegetation types. All forms are haunters of primary and secondary forest or man-made plantations, and are not found in open country.

(2) The breeding place of *A. l. balabacensis* is described in detail, the typical site being a small pool, or group of pools, with fairly clean seepage or rain-water, still or with very slight flow, and under some degree of shade ; direct sunlight from the period 9 a.m. to 3 p.m. appears to inhibit breeding. Most breeding places occur in the clay soil typically associated with hilly country. Breeding pools are commonly formed by human and animal activities, and a considerable proportion of the larval population occurs in rather open and temporary sites. Of the remaining forms, the breeding places of *l. leucosphyrus*, *pujutensis*, and the " Celebes form " resemble that of *l. balabacensis*, while the others occupy more specialised niches.

(3) The results of removing shading vegetation from around breeding places of *balabacensis* are described and it is shown that the subsequent disappearance of breeding is gradual and not due to any direct effect of light upon the ovipositing female ; presumably changes in the nature of the water in the pools make them unattractive.

(4) Notes are given on the collecting and rearing of larvae ; also observations suggesting that larvae, under natural conditions, are rather insensitive to pH and light conditions.

(5) All members of the group are " wild " species, not resting by day inside houses. Several outdoor resting sites of *A. l. balabacensis* are described, in a rubber plantation and in secondary jungle.

(6) *A. l. balabacensis* is a late feeder, with a peak after midnight. Unfed females tend to congregate outside houses quite early in the night and rest on foliage, etc., some for long periods, before entering. By comparison with other species, however, there is little actual aversion to entering houses. After entry, some 50 per cent. rest on the walls before feeding but, after feeding, almost all do so ; when fed, the resting period appears to increase throughout the night and may be as long as three hours. There is a noticeable tendency to attack in waves ; also a tendency for outdoor catches to be correlated with moonlight—catches between 8 and 11 p.m. were greatest during the period first quarter to full moon, and least during the last quarter to new moon. The behaviour of *A. l. leucosphyrus* is, as far as known, virtually identical with that of *l. balabacensis*.

(7) The available information regarding *l. balabacensis* and *l. leucosphyrus* is pooled to form some picture of the behaviour patterns which interact to produce the feeding cycle. The initial activation to flight activity is possibly a release of the inhibiting effect of light, and it seems probable that the mosquito then flies at random, or orientated by physical factors, such as wind currents. Although conclusive evidence is lacking, it seems likely that direct orientation, by and towards the host, operates over short distances only, *i.e.* there is no long-range attraction ; also that the unfed females found resting near the host have been deactivated by their *initial* contact with vapours, etc., emanating

from it. During this resting period, attractant stimuli re-activate the mosquito to the level at which feeding takes place. Similarly, after feeding the engorged mosquito must again rest until it has attained the level of activation required to cause or allow exit. Mechanisms which might produce this course of events are discussed, and the general hypothesis is shown to explain most of the known facts, including, for instance, the tendency to attack in waves.

(8) There is strong evidence that both *l. balabacensis* and *l. leucosphyrus* have a distinct preference for human blood ; the " Celebes form " also attacks humans. Of other forms, *hackeri*, *pujutensis* and *riparis* all show a complete indifference or aversion to human baits.

(9) Adult densities of *A. l. balabacensis*, and probably most other forms, are correlated with rainfall, due to the nature of their breeding places and, in *l. balabacensis* at least, to the effects of humidity upon adult survival. In the case of *balabacensis*, not only adult numbers but the sporozoite rate also tend to increase in wet weather.

(10) The known vectors of human malaria are *A. l. balabacensis*, *A. l. leucosphyrus* and the " Celebes form "; the first in North Borneo, Burma, Assam and Indo-China ; the second in Sarawak, Sumatra and almost certainly in Indonesian Borneo also ; the third in Celebes and adjacent islands. Other forms of *A. leucosphyrus* sens. strict. may be dangerous, but the remaining members of the group are almost certainly harmless.

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